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Taxonomy, Phylogeny and Biogeography of *Asterocampa* Röber 1916

(Lepidoptera, Nymphalidae, Apaturinae)

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Preface

The material presented here is taken from my dissertation entitled, "A taxonomic revision of *Asterocampa* Röber 1916 (Insecta, Lepidoptera, Nymphalidae)," accepted in partial fulfillment of a doctoral degree in entomology by the Graduate School of Texas A&M University, May 1985. Aside from corrections, I have added new and clarifying material in the past two years, largely as a result of morphological investigations of other closely related genera.

My special interest in hackberry butterflies stems from observations I made on insects inhabiting hackberry trees at the Brackenridge Field Station of the University of Texas in Austin, while I was a graduate student there. Many a day (and several nights) were spent observing larvae and adults in an attempt to figure out how the two resident species of *Asterocampa* and other hackberry insects partitioned resources. My move to Texas A&M University (systematic entomology) and choice of doctoral dissertation were direct outgrowths of those early studies.

The hackberry butterflies, *Asterocampa* Röber, are here taxonomically revised based on biological and morphological studies of all life stages of these insects. A new subspecies name is proposed for the Floridian population of *Asterocampa celtis* (Boisduval & Le Conte) which has mistakenly been called *A. alicia* (Edwards). There are conservatively four biological species of hackberry butterflies, based on field observations, preliminary laboratory hybridization studies, and morphological comparisons.

The geographic ranges of the species in the genus extend from Nicaragua and the Greater Antilles, north and westward through Mexico and the United States (except the Pacific Northwest) into southeastern Canada. The butterflies are typically found in close association with hackberry (Ulmaceae: *Celtis* spp.) which is their sole larval food plant.

Cladistic methodology was employed to construct the classification presented. *Asterocampa* is defined in relation to other apaturine genera. The evolution of the genus is discussed in the context of the distributions of the taxa. *Asterocampa* probably evolved in North America following its introduction and subsequent isolation from eastern Asia. There are 2 well-defined species groups in the genus, which utilize the host plant in different ways.

These studies would not have been possible but for the many people from whom I have received help or advice. I thank P. R. Ackery, C. R. Beutelspacher, F. M. Brown, H. R. Burke, J. M. Burns, J. R. Cate, J. P. Donahue, W. D. Duckworth, C. Durden, G. Ekis, J. F. Emmel, C. D. Ferris, L. E. Gilbert, D. W. Jenkins, K. Johnson, G. Lamas, L. D. & J. Y. Miller, R. W. Neck, S. J. Ramos, J. E. Rawlins, W. J. Reinthal†, F. Rindge, D. H. Riskind, R. K. Robbins, J. C. Schaffner, D. J. Schmidly, A.

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Introduction

Asterocampa Röber is a genus of North American butterflies, the members of which are known as hackberry butterflies. There are roughly a dozen species-level taxa of hackberry butterflies. Taxonomically, they belong in the family Nymphalidae (sensu latu) or in the Apaturidae, a closely related family of butterflies whose members are somewhat intermediate in morphology between the Nymphalidae (sensu strictu) and the Satyridae. There are about 20 apaturine genera, all in the Old World, except for the Nearctic *Asterocampa* and the Neotropical *Doxocopa* Hübner.

Asterocampa larvae feed on hackberry trees and shrubs (*Celtis* spp., Ulmaceae), from which the adult common name is derived. Hackberry butterflies occur from Nicaragua and the Greater Antilles north and westward through Mexico and the United States (except the Pacific Northwest) and into southeastern Canada, virtually everywhere their larval host plants occur.

Asterocampa was badly in need of revision, not having been broadly treated since the apaturine butterflies were catalogued in 1938 (Stichel, 1938). Recognizing this need, the late Dr. Walfried J. Reinthal studied hackberry butterflies over the last 3 decades with the intention of revising the genus. His extensive fieldwork in the United States and the Caribbean, coupled with rearing and breeding studies, gave him a unique appreciation for the diversity within the genus. Although he was never able to summarize his findings for publication, authors treating these butterflies in the last 20 years have relied on his extensive knowledge of the genus in their books and articles (Brown, 1967; Comstock, 1961; dos Passos, 1964; Howe, 1975; Johnson and Nixon, 1967; Miller and Brown, 1981, 1983; Pyle, 1981). As a consequence, the best evidence supporting the present classification of *Asterocampa* is found in the collection of reared specimens, notes and correspondence of Dr. Reinthal. This collection was willed to the Carnegie Museum of Natural History.

There are three purposes to my revision of hackberry butterflies. First, the recognizable species-level taxa of *Asterocampa* are defined, described, ranked and related. Second, the genus is defined by synapomorphic characters (Hennig, 1966; Wiley, 1981). A testable hypothesis is made about its closest relatives, or sister group. Third, ecologic and biogeographic hypotheses are formed, relating the character diversity and distributions of hackberry butterflies.

My approach to this revision is cladistic in the sense of Wiley (1981). Morphological and behavioral characters of all developmental stages of hackberry butterflies are surveyed. As many characters as could be reliably compared with those found for other apaturine genera are used as a starting point from which to define *Asterocampa*. Material from major North American museums was borrowed for examination. All but one taxon was reared so that living specimens were studied for virtually all hackberry butterflies in all their life stages.

Taxonomic History

The taxonomic history of hackberry butterflies is complex for the size of their genus. Taxa presently assigned to *Asterocampa* have resided in a half dozen genera over the years. Application of species-level names to these taxa has been a source of controversy for over a century. The genus *Asterocampa* was proposed by Röber in 1916 in Seitz's *Macrolepidoptera of the World*, the first name to include just the North American New World apaturine butterflies.

A sketch of nomenclatural changes through major North American works is given in tabular form (Table 2) below the table of Röber's included taxa (Table 1). For a more complete treatment of the nomenclatural history of hackberry butterflies the reader should refer to my dissertation.

The common names applied to species and subspecies now included in *Asterocampa* are an interesting sideline to the history of the group. Riley (1873) first called the genus "hackberry butterflies." For a complete treatment of these names the reader should refer to my dissertation.

Table 1. Hackberry butterflies treated by Röber *in* Seitz (1916).

Date	**Taxon as described**	**Taxa**, according to Röber (1916)
1793	*Papilio lycaon* Fabricius	*Asterocampa lycaon* Fab.
1793	*Papilio herse* Fabricius	*A. lycaon* Fab.
[1828]	*Doxocopa idyja* Geyer *in* Hübner	**A. lycaon form idyja Hbn.**
[1835]	*Apatura celtis* Boisduval & Le Conte	**Asterocampa celtis Bsd.**
[1835]	*Apatura clyton* Boisduval & Le Conte	*A. lycaon*. Fab.
1864	*Apatura argus* Bates	**Asterocampa argus Bates**
1868	*Apatura alicia* Edwards	**Asterocampa alicia Edw.**
1868	*Apatura proserpina* Scudder	*A. lycaon* Fab.
1874	*Apatura leilia* Edwards	**Asterocampa leilia Edw.**
1876	*Apatura clyton* var. *ocellata* Edwards	*A. lycaon* aberr. *ocellata* Edw.
1876	*Apatura clyton* var. *flora* Edwards	**A. lycaon form flora Edw.**
[1878]	*Apatura antonia* Edwards	**A. leilia [form] antonia Edw.**
1883	*Apatura antonia* var. *montis* Edwards	**A. celtis [form] montis Edw.**
1911	*Chlorippe clyton* var. *texana* Skinner	*A. lycaon* Fab.
1912	*Doxocopa argus* form *armilla* Fruhstsorfer	*A. argus* [color f.] *armilla* Fru.

Table 2. Comparison of American classifications of hackberry butterflies.

Skinner, 1911	**McDunnough, 1938**	**Miller & Brown, 1983**	**Present revision**
1. celtis	1. celtis	1. celtis	1. celtis
a. alicia	a. alicia	2. alicia	a. reinthali
b. antonia	b. antonia	3. antonia	b. antonia
	c. montis	4. montis	
c. leilia	2. leilia	5. leilia	2. leilia
		a. cocles	
2. clyton	3. clyton	6. clyton	3. clyton
a. flora	a. flora	7. flora	a. flora
b. texana	b. texana	8. texana	b. texana
	c. subpallida	9. subpallida	
		10. louisa	c. louisa
		[11. idyja]	4. idyja
		[12. argus]	a. argus

Table 3. Classification of *Asterocampa* Röber.

Asterocampa Röber, 1916. *In* Seitz, Großschmett. Erde, 5: 549. Type-species by subsequent designation of D. M. Bates, 1926. Entomol. News, 37: 154, *Apatura celtis* Boisduval and Le Conte, [1835]. Hist. gen. iconogr. lépid. amér. sept.: 210.

1. **celtis** (Boisduval and Le Conte, [1835]) *APATURA*. Hist. gen. iconogr. lépid. amér. sept.: 210. TL - "Géorgie", probably northwest of Savannah, perhaps in Screven County, Georgia. Type based on Abbot drawing, the model for which has not been found.
   a. c. **celtis** (Boisduval and Le Conte, [1835]). [as above]
   = **alicia** (W. H. Edwards, 1868) *APATURA*. Butts. N. Amer., 1: [135]. TL - vic. New Orleans, Louisiana. Types lost; the figures in W. H. Edwards, 1868. Butts. N. Amer., 1: pl. Apatura I may be considered to represent types.
   = **alba** (W. G. Wright, 1905) *APATURA*. Butts. W. Coast: 58. Validating excluded name "Celtis ab. a. Alb." (H. Strecker, 1878) *APATURA*. Butts. moths N. Amer.: 145. TL not stated, but may be taken as Coalburgh, West Virginia. Type represented by Edwards' figure, 1875. Butts. N. Amer., 2: pl. Apatura I, fig. 5.
   b. c. **reinthali** Friedlander, 1987. [this work] TL - Ocoee, Florida. HT to be placed in CMNH.
   c. c. **antonia** (W. H. Edwards, [1878]). *APATURA*. Field and Forest, 3:103. TL - vic. Norse, Bosque Co., Texas, restricted by F. M. Brown, 1967. Trans. Amer. Entomol. Soc., 93: 377-378. LT in CMNH, designated by F. M. Brown, 1967. Trans. Amer. Entomol. Soc., 94: 379.

= **montis** (W. H. Edwards, 1883) *APATURA*, Papilio, 3:7. TL - vic. Ft. Grant, Graham Mtn., Cochise Co., Arizona. LT in CMNH, designed by F. M. Brown, 1967. Trans. Amer. Entomol. Soc., 93: 382.

2. **leilia** (W. H. Edwards, 1874) *APATURA*. Trans. Amer. Entomol. Soc., 5: 103. TL - "Camp Lowell and in Sonoto Valley, Arizona". LT in CMNH, designated by F. M. Brown, 1967. Trans. Amer. Entomol. Soc., 93: 385.

= **cocles** (Lintner, (1885)) *APATURA*. Papilio, 4: 141. TL - Hidalgo, Texas. LT in CMNH [designated in this work].

3. **clyton** (Boisduval and Le Conte, [1835]) *APATURA*. Hist. gen. iconogr. lépid. amér. sept.: 208. TL - "méridionales des États-Unìs", probably Screven County, Georgia. Type based on Abbot drawing, the model for which has not been found.

a. **c. clyton** (Boisduval and Le Conte, [1835]). [as above]

= **ocellata** (W. H. Edwards, 1876) *APATURA*. Butts. N. Amer., 2: [245]. TL - Coalburgh, West Virginia. LT in CMNH, designated by F. M. Brown, 1967. Trans. Amer. Entomol. Soc., 93: 387.

= **proserpina** (Scudder, 1868) *APATURA*. Proc. Boston Soc. Nat., Hist., 11: 401. TL - Iowa. Type misplaced; not in MCZ.

= **nig** (J. B. Smith, 1903) *APATURA*. Check list Lepid. bor. Amer.: 4. Validating excluded name "Clyton ab. b. Nig." (H. Strecker, 1878) *APATURA*. Butts. moths N. Amer.: 145. TL - Berks Co., Pennsylvania. HT in Strecker Coll. presently located at AME.

b. **c. flora** (W. H. Edwards, 1876) *APATURA*. Butts. N. Amer., 2: [247]. TL - Palatka, Florida. LT in CMNH, designated by F. M. Brown, 1967. Trans. Amer. Entomol. Soc., 93: 389.

c. **c. texana** (Skinner, 1911) *CHLORIPPE*. Trans. Amer. Entomol. Soc., 37: 214. TL - Round Mt., Texas. HT in CMNH.

= **subpallida** (Barnes and McDunnough, 1913) *CHLORIPPE*. Contr. Nat. Hist. Lepid. N. Amer., 2: 99. TL - Babaquivera [*sic*] Mtns., Pima Co., Arizona. LT in USNMNH [designated in this work].

d. **c. louisa** Stallings and Turner, 1947. Entomol. News, 58: 38. TL -Pharr, Texas, HT in YPM.

4. **idyja** (Geyer, [1828]) *DOXOCOPA*. *In* Hübner, Samml. exot. Schmett., 3: pl. [13]. TL - Cuba. Type presumably lost; the figures considered to represent type.

a. **i. idyja** (Geyer). [as above]

= **padola** (Fruhstorfer, 1912) *DOXOCOPA*. Entomol. Rundschau, 29: 14. TL - Haiti. STs in ZMHU, Berlin.

b. **i. argus** (H. W. Bates, 1864) *APATURA*. Entomol. Month. Mag., 1: 130. TL - Motagua Valley, Guatemala. HT in BM.

Keys for the Identification of Species and Subspecies of *Asterocampa*

EGGS:

1. Eggs deposited singly or in small clusters (1-50); with wrinkling of chorion between longitudinal ribs and with aeropyles along whole length of ribs to base (Pl.5, fig. B; Pl.6, fig. C; Pl.8, fig. C).. 2

1′. Eggs deposited in large tightly packed clusters forming multilayered egg mass, often 3- to 5-layered (50-500); without wrinkling of chorion between longitudinal ribs and lacking aeropyles on lower half of ribs (Pl.13, figs. C, D; Pl.14, figs. C, D; Pl.16, fig. B)... 6

2. Eggs deposited on tree-like hackberry species (*Celtis occidentalis, C. tenuifolia, C. laevigata, C. lindheimeri, C. reticulata*).. 3

2′. Eggs deposited on spiny hackberry species (*Celtis pallida*)........ 4

3. Eggs deposited on host plant from eastern North America (east of 100°w. longitude).. 5

3′. Eggs deposited on *Celtis reticulata* (west of 100°w. longitude)... ***Asterocampa celtis antonia***

4. Eggs with aeropyles not reduced (Pl.6, fig. C)... ***Asterocampa celtis antonia*** (part)

4′. Eggs with extremely small aeropyles (Pl.8, fig. C)... ***Asterocampa leilia***

5. Eggs occurring in eastern North America but not found in peninsular Florida, coastal Georgia or South Carolina.. ***Asterocampa celtis celtis***

5′. Eggs on *Celtis laevigata* in peninsular Florida, coastal Georgia or South Carolina.......................... ***Asterocampa celtis reinthali***

6. Eggs found north of Tropic of Cancer.. 7

6′. Eggs found south of Tropic of Cancer...................................... 10

7. Eggs deposited on *Celtis reticulata, C. lindheimeri* or *C. laevigata*, found in central, south or west Texas, Mexico or Arizona........... 8

7′. Eggs deposited on *Celtis laevigata, C. occidentalis* or *C. tenuifolia*, found in east and northeast Texas, northward and eastward... 9

8. Eggs found in northeastern Mexico or lower Rio Grande Valley of Texas.. ***Asterocampa clyton louisa***

8′. Eggs found in south-central or west Texas, north-central Mexico around the edges of the Chihuahuan desert, or southeastern Arizona... ***Asterocampa clyton texana***

8″. Eggs found in northwestern Mexico (central Sonora).. ***Asterocampa idyja argus*** (part)

9. Eggs occurring in eastern North America but not found in

peninsular Florida, coastal Georgia or South Carolina .... ***Asterocampa clyton clyton***

9′. Eggs on *Celtis laevigata* in peninsular Florida, coastal Georgia or South Carolina .... ***Asterocampa clyton flora***

10. Eggs occurring in Mexico or Central America .... ***Asterocampa idyja argus***

10′. Eggs on *Celtis trinervia* in the Greater Antilles .... ***Asterocampa idyja idyja***

LARVAE:

1. Larvae not aggregated as early instars (except diapausing third instars); with antler scolus AB5 (Fig. 1; Pl.7, figs. A, C; Pl.10, figs. A, C; Pl.11, figs. A, C, E) at most half the length of head scolus L1 (first instar larvae with dark brown or black head capsules, found in small numbers associated with small egg clusters); never longitudinally banded, but usually striped with lines and crenations of light yellow **2**

1′. Larvae gregarious as first 3 instars; with antler scolus AB5 (Fig. 1; Pl.15, figs. A, B; Pl.16, figs. C-E) more than half the length of head scolus L1 (first instar larvae generally with light brown or tan head capsules, found in large numbers associated with large egg mass); often longitudinally banded with light yellow and green **5**

2. Larvae not on *Celtis pallida*; mature larva usually marked with yellowish spots anterodorsally and zigzag (crenated) yellowish line laterally on abdominal segments **3**

2′. Larvae on *Celtis pallida*, mature larva usually marked with only dorsolateral and subspiracular yellowish lines on body **4**

3. Larvae exceptionally with vestigial antler scolus AB5; usually found on *Celtis reticulata* ....***Asterocampa celtis antonia***

3′. Larvae usually with vestigial antler scolus AB5; usually found on *Celtis laevigata*, *C. occidentalis*, or *C. tenuifolia* .... eastern subspecies of ***Asterocampa celtis***

4. Larva found in south Texas or northeastern Mexico; mature larva with black head marked with yellowish green .... ***Asterocampa celtis antonia*** (part)

4′. Larva found west of 100° west longitude, or mature larva with brown head marked with green and yellowish white .... ***Asterocampa leilia***

5. Larvae without black anal horns; generally found north of Tropic of Cancer **6**

5′. Larvae usually with black anal horns; found in Mexico, Central America and Greater Antilles .... subspecies of ***Asterocampa idyja***

6. Larvae generally not banded with yellow and green; usually found on *Celtis reticulata* in Texas, Mexico or Arizona................ 7
6′. Larvae generally banded with yellow and green; usually found on *Celtis occidentalis, C. laevigata* or *C. tenuifolia* in eastern United States............. eastern subspecies of ***Asterocampa clyton***
7. Larvae found in northeastern Mexico or lower Rio Grande Valley of Texas (sometimes with rudimentary banding, often colorful, with dark heads and yellow and green bodies) ....***Asterocampa clyton louisa***
7′. Larvae found in south-central or west Texas, north-central Mexico around the edges of the Chihuahuan desert, or southeasten Arizona (usually mostly green with whitish markings and only a small dark brown spot anteriorly on the antlers) .... ***Asterocampa clyton texana***

PUPAE:

1. Pupae with rather pointed pyramidal head prologations; dorsal crest not abrupt from thorax to abdomen, with blunt spines anteriorly on abdominal segments 3-8 (Pl.19, figs. G-J; Pl.11, fig. F; Pl.12, fig. D)... 2
1′. Pupae with blunt pyramidal head prolongations; dorsal crest often rising abruptly at third abdominal segment, generally with sharp spines anteriorly on abdominal segments 3-8 (Pl.19, figs. K, L)... 3
2. Pupae with bed of cremastral hooks extending to end of sustainers in "Y"-shaped pattern; head prolongations long ....***Asterocampa celtis*** subspecies
2′. Pupae with bed of cremastral hooks extending only half way to sustainers (Pl.12, figs. D, E; Pl.19, fig. J); head prolongations very short..***Asterocampa leilia***
3. Pupae without shortened metanotum dorsally............................ .... ***Asterocampa clyton*** subspecies
3′. Pupae with shortened metanotum dorsally .... ***Asteocampa idyja*** subspecies

ADULTS:

1. Forewings with dark brown limbal spots in cell Cu1, eyespot present on hindwing anal cup ventrally (cell A2 limbal spot) (Fig. 2); male genitalia with saccus and aedeagus usually less than twice length of valves, uncus shallowly indented; female genitalia with short ductus (Figs. 3, 6), signa usually present 2

1′. Forewings without dark brown limbal spot in cell Cu1 (although spots might be narrowly ringed in dark brown), no eyespot on hindwing anal cup ventrally (Fig. 2); male genitalia with saccus and aedeagus at least 2 times length of valves, uncus narrowly notched; female genitalia with long ductus (Figs. 6, 7), signa usually absent **5**

2. Forewings without broken basal discal bar; terminal dorsal brush with straight hair-scales (Pl.21, figs. A-C) ....***Asterocampa leilia***

2′. Forewings with broken basal discal bar (forming 2 spots); terminal dorsal brush with recurved hair-scales **3**

3. Forewing with dark brown limbal spot in cell M3, both it and Cu1 with pupils, limbal spot Cu1 about equal in size to M3, or even smaller (Pl.19, figs. M, N; Pl.20, figs. G-O)........................... .... ***Asterocampa celtis antonia***

3′ Forewing without dark brown limbal spots in cell M3 or with at most posterior portion of spot M3 narrowly ringed with brown, limbal spot Cu1 generally larger than M3 and unpupilled.......... **4**

4. Not especially large (average FW costal length 24 mm (males), 27 mm (females)); pupils of limbal spots not particularly large or colorful, pupil of spot Cu1 of FW centered, spot M1 of HW round to oval and not elongated into a point laterally (Pl.20, figs. A-C).... .... ***Asterocampa celtis celtis***

4′ Noticeably large (average FW costal length 29 mm (males), 31 mm (females)); pupils of limbal spots large and light blue or blue green, spot Cu1 of FW lateralized, spot M1 of HW asymmetrically elongate with crescentic pupil (Pl.20, figs. D-F) ... .***Asterocampa celtis reinthali***

5. Postmedian spots in normal zigzag positions (Fig. 2), those anterior in forewings lying between end of discal cell and limbal spots.. **6**

5′. Postmedian spots shifted basally in anterior portion of forewings, next to end of discal cell (Pl.22, figs. J, L) **9**

6. Limbal spot Cu1 of forewing usually narrowly ringed with dark brown, neither sex noticeably dimorphic in color, usually a high percentage of females with hindwing limbal spots ventrally not being fully expressed **7**

6′. Limbal spots Cu1 of forewing virtually never ringed with dark brown, both sexes often exhibiting dark and light color phases, ventral hindwing limbal spots in females usually fully expressed.. **8**

7. Ground color of apical forewings and dorsal coloration of antennae brown or orange, not black; found in south-central and west Texas, in foothills of the Chihuahuan desert and in southeastern Arizona (not found in lower Rio Grande Valley of Texas and southward into northeastern Mexico) (Pl.21,

figs. M-O; Pl.22, figs. A-C) .... ***Asterocampa clyton texana***

7.′ Ground color of apical forewings and dorsal coloration of antennae black; found in lower Rio Grande Valley of Texas and southward into northeastern Mexico (Pl.19, fig. O; Pl.22, figs. D-F) .... ***Asterocampa clyton louisa***

8. Not especially large (average FW costal length 25 mm (males), 31 mm (females)); apical ground color of forewings tan to brownish orange, light and dark color phase individuals present in varying percentages, hindwing limbal spots ventrally usually fully expressed (Pl.21, figs. D-I); not found in peninsular Florida, coastal Georgia or south coastal South Carolina .... ***Asterocampa clyton clyton***

8′. Noticeably large (average FW costal length 27 mm (males), 34 mm (females)); apical ground color of forewings bright reddish orange, dark color phase virtually absent, hindwing limbal spots ventrally often not fully expressed (Pl.21, figs. J-L); occurs in peninsular Florida, coastal Georgia or south coastal South Carolina (occasional phenocopies along Gulf) .... ***Asterocampa clyton flora***

9. Occur in Mexico or Central America; individuals usually have postmedian spots coalesced into golden band across FW, dark phase individuals not exhibiting this feature (Pl.22, figs. G-I) .... ***Asterocampa idyja argus***

9′. Occur in Cuba, Hispaniola or Puerto Rico; light to dark individuals, but none exhibiting golden band across FW (Pl.22, figs. J-O) .... ***Asterocampa idyja idyja***

Species and Subspecies Concepts of Hackberry Butterflies

Hackberry butterfly species were investigated within the context of the concept of biological species. Different species are said to be reproductively isolated from one another and populations of a single species are not, even though these populations might be allopatric or allochronic with regard to one another. This study is admittedly one of morphology and behavior, but very little of the latter was actually observed that would give needed evidence in this discussion. Molecular techniques involving the following of genetic markers through natural and laboratory breeding experiments are needed to refine what is postulated here.

Questions asked here are: 1) Do sympatric, synchronic populations of reputedly different species of hackberry butterflies interbreed in the field or the laboratory? 2) Do allopatric populations of what are currently held as species interbreed in the laboratory? 3) Are there either morphological or behavioral characteristics of any of the hackberry butterflies that might reasonably prevent them from interbreeding with other such populations (isolating mechanisms)? 4) Are there "hybrid populations" to be found in the field that offer evidence of genetic exchange between allopatric (or stasipatric) populations?

Viewed cladistically, the ability to interbreed is a character shared before speciation and not necessarily lost at speciation (symplesiomorphy). Only the inability to interbreed "in the wild" is held as acceptable as an indication that the respective populations under consideration belong to different species. The problems associated with allopatric and allochronic populations being compared or tested for the ability to interbreed have often been noted (e.g., Ehrlich, 1961). It is the opinion here that obstructions to interbreeding owing to differences in the organisms (and not the testing conditions) might serve to indicate respective specific status of the different populations being tested.

The known distributions of taxa studied in this revision are presented graphically in Plates 1-4. *Asterocampa celtis* and *A. clyton* are broadly sympatric over much of their respective ranges. Both of these species are sympatric with *A. leilia* over much of its range.

The degrees to which organisms are reproductively isolated have been argued to greater and lesser extents to indicate biological species (e.g., Mayr, 1969; H. H. Ross, 1974). One can only speculate whether or not a small degree of genetic exchange will lead the populations to speciation, or whether or not climatic or other conditions might change soon enough to affect their status (in either direction). A conservative approach has been taken in this revision. Unless it can be shown that the populations at hand are probably reproductively isolated, they are considered to be conspecific.

Sympatric and at least partially synchronic populations of hackberry butterflies are listed in Table 4.

Table 4. Sympatric populations of hackberry butterflies and examples of localities in which they can be found.

Localities	**Populations of Hackberry Butterflies**
wash at base of mountain in southeastern Arizona	*A. leilia, A. celtis antonia* ("montis"), *A. clyton texana* ("subpallida")
creek bottom in the chaparral of south Texas	*A. leilia* ("cocles"), *A. celtis antonia, A. clyton texana* or *A. clyton louisa*
Knoxville, Tennessee, or just about anywhere in e. U. S.	*A. celtis celtis, A clyton clyton*
south of New Orleans, Louisiana	*A. celtis celtis* ("alicia"), *A. clyton clyton* (form similar in appearance to *A. c. flora*)
Ocoee, Florida	*A. celtis reinthali, A. clyton flora*

No interbreeding of butterflies from different populations at any of these and other localities was ever observed. Intra-population matings have been observed in the field for all the taxa in Table 4. Behavioral differences among sympatric populations were observed at these sites, which might help explain why no inter-pairings were seen.

Sympatric hackberry butterflies seem to be ecologically separable along 2 lines. The first line is exemplified by *A. leilia*. It has its own particular species of host plant which grows in a slightly different habitat than hosts used by other hackberry butterflies at a given site.

Males of hackberry butterflies perch within and rarely patrol a small area usually containing the larval food plant (Austin, 1977; Scott, 1975; personal obs.) and intercept virtually all passers-by in search of females. This is reasonable because virgin females emerge from pupal cases on the larval food plants and visit food sources near the future oviposition sites. However, in the case of *A. leilia*, the micro-habitat in which males perch is generally the ground in a dry wash. Males of other species of *Asterocampa* at the site would more likely be perched on trees growing in the wetter parts of the wash and would investigate different passers-by.

By far the most likely micro-habitat in which different species would be found together is at a rich food source such as a sap ooze on mesquite. Individuals at the ooze would be of both sexes but the females would have generally been previously mated and plugged.

The second line of ecological evidence for habitat partitioning by hackberry butterflies stems from the time of day the different species are active. This is best seen by times in which males from different sympatric populations are involved in courtship. In virtually every instance of observation, peak activity of one would be at mid-day and the other in the evening. It is worth putting forward the hypothesis that members of the Clyton group are active at higher temperatures than those of the Celtis group. In more southern localities one generally finds individuals of the Clyton group active at mid-day and those of the Celtis group active in the evening. The situation seems to be reversed in more northern localities, as individuals of the Celtis group are active at mid-day while individuals of the Clyton group are active in the late afternoon. It is rare to find males of different populations actively engaged in courtship at the same time and place.

A possible third instance of ecological separation stems from the observation that males of the Celtis group are often found within the canopy of the forest, whereas males of the Clyton group are more often found on the outside of the canopy. This difference might also be due to behavioral differences related to temperature.

A possible fourth ecologically important difference between sympatric populations of hackberry butterflies, one that also relates to courtship, is the difference in coloration in adults of the species. The only case in which there are two phenotypically very similar species occurring together is that of *A. leilia* and *A. celtis antonia* from Arizona to southern Texas.

A more complete study of the genetic differentiation of the hackberry butterflies such as was done by Hafernik (1982) for the North American buckeye butterflies (Nymphalidae: *Junonia* spp.) was not possible within the limitations of this revision. However, some data on the ability of different populations to exchange genetic information was found through hybridization studies. A complete regimen of crosses within and between different species, with the associated data of viabilities for each life stage was not attempted.

Laboratory populations were established for crossing, including the following taxa from the given localities: *A. celtis antonia* (Eddy Co., N Mex.) (virgin females challenged with wild males of *A. celtis celtis* from Brazos Co., Texas); *A. clyton louisa* (Hidalgo Co., Texas) (virgin females challenged with wild males of *A. clyton clyton* from Brazos Co., Texas); *A. clyton clyton* (Brazos Co., Texas) (challenged with reared individuals of *A. celtis celtis* (Brazos Co., Texas)); *A clyton texana* (Menard Co., Texas) (challenged with virgin males of *A. celtis antonia* (Eddy Co., N. Mex.). Only the first 2 crosses were successful, and the adult hybrid butterflies were reared.

Individuals of the following populations were reared and subjected to breeding challenges: *A. celtis antonia* (Travis Co., Texas) (by *A. clyton texana* (Travis Co., Texas)); *A celtis celtis* (Brazos Co., Texas) (by *A. clyton clyton* (Brazos Co., Texas)); *A celtis antonia* (Jeff Davis Co., Texas) (by *A clyton texana* (Jeff Davis Co. Texas)); *A celtis antonia* form "montis" (Pima Co., Arizona) (by *A. clyton texana* ("subpallida") (Pima Co., Arizona)); *A clyton flora* (Alachua Co., Florida) (by *A. celtis reinthali* (Alachua Co., Florida). None of these attempted crosses were successful.

In similar studies conducted by Dr. Walfried J. Reinthal (unpublished data) the following crosses (with back-crosses) were obtained: *A. celtis antonia* (Woodward Co., Oklahoma) (by *A. celtis antonia* ("montis") (Graham Co., Arizona)); *A. celtis antonia* (Palo Pinto Co., Texas) (by *A. celtis celtis* (Bibb Co., Georgia)). Attempts by him to cross members of the Clyton group with those of the Celtis group, like those of this author and many amateur breeders of butterflies, failed.

Successful crosses (viable adults reared in quantity) have been attained for the pairs of hackberry butterflies listed in Table 5.

Hybrid adult butterflies are phenotypically intermediate in characters used in that stage to define the parental types. This observation prompted the search (actually a feed-back loop) for similar looking wild butterflies in geographic areas between adjacent taxa. If one believes that observed intermediate phenotypes are indicative of hybridization in the field (not necessarily true!), there is hybridization between many pairs of taxa. In some cases there are zones of presumed hybridization between taxa in bands of many hundreds of kilometers long with varying thicknesses. These hypothesized bands of intergradation need

Table 5. Successful crosses between taxa of *Asterocampa*.

Challenged Female		**Challenging Male**	**Breeder**
A. celtis antonia (“**montis**”)	X	*A. celtis* ***antonia***	Reinthal
A. celtis ***antonia***	X	*A. celtis antonia* (“**montis**”)	Reinthal
A. celtis ***antonia***	X	*A. celtis* ***celtis***	Friedlander, Reinthal
A. celtis ***celtis***	X	*A. celtis* ***antonia***	Friedlander, Reinthal
A. clyton ***louisa***	X	*A. clyton* ***clyton***	Friedlander

documentation by genetic means. One such band between subspecies of *A. celtis*, extends from near San Antonio, Texas to northwestern Nebraska, zigzagging its way through Oklahoma, Kansas and Colorado. Notably, in Austin, Texas and Denver, Colorado, populations of *A. celtis* exhibit the whole range in phenotypes between *A. celtis celtis and A. celtis antonia.* Similar zones of intergradation occur for the pairs of hackberry butterflies shown in Table 6.

Table 6. Pairs of hackberry butterflies for which populations showing intermediate characters have been observed in geographically intermediate areas.

Taxa: 1	**2**	**Location of Intermediates**
A clyton texana	*A. clyton texana* (“subpallida”)	Chihuahuan desert edges
A. clyton texana	*A. clyton louisa*	upper Rio Grande Valley
A. clyton texana	*A. clyton clyton*	e. Texas to e. Kansas
A. clyton clyton	*A clyton flora*	coastal Georgia, Florida panhandle to Louisiana
A. celtis antonia	*A. celtis antonia* (“montis”)	central New Mexico, w. Texas
A. celtis antonia	*A. celtis celtis*	central Texas to nw. Nebraska
A. celtis celtis	*A. celtis celtis* (“alicia”)	e. Texas to s. Mississippi
A. celtis celtis	*A. celtis reinthali*	coastal Georgia, Florida panhandle

Nothing is known about the ability of either *A. leilia* or *A. idyja* to interbreed with other hackberry butterflies. It is possible that *A. leilia* could form hybrids with *A. celtis antonia*, but no wild intermediate butterflies have been called to anyone’s attention. It is also possible that

A. clyton texana in one of its forms could come into contact with and possibly interbreed with *A. idyja argus* in either northeastern or northwestern Mexico. There are no intermediate forms known. To my knowledge, *A. idyja idyja* has not been reared during the past 50 years.

In summary, the presumed interfertile taxa are presented in Table 7.

Table 7. Interfertile taxa (4 species) of hackberry butterflies.

Celtis group	**Clyton group**
A. celtis antonia	*A. clyton texana*
A. celtis antonia (= "montis")	*A. clyton texana* (= 'subpallida")
A. celtis celtis	*A. clyton louisa*
A. celtis celtis (= "alicia")	*A. clyton clyton*
A. celtis reinthali	*A. clyton flora*
A. leilia	*A. idyja idyja*
A. leilia (= "cocles")	*A. idyja argus*

Populations of infraspecific rank which are well defined geographically and distinguishable by some other set of characters are called separate subspecies in this revision. The subspecies is the lowest ranked taxon.

If such a population shows a gradual cline or a step-cline over a long distance with its neighbor, it is considered as not being well defined geographically. The Texan and eastern Mexican populations of *Asterocampa leilia* and the Rio Grande Valley (Texas, Mexico) population of *A. celtis antonia* are not considered subspecies in this revision. These populations have the informal names of "cocles" and "mexicana," respectively. I consider these as being taxa worth referring to by separate names, but not worthy of separate, valid, scientific names. Other distinctive populations of hackberry butterflies at the edges of their respective species' ranges include "montis" and "subpallida" in Arizona. Many other such populations exist but have not been given names. These are probably best handled by giving the locality of the population in question when discussing it, for example, "the Lake Roosevelt, Arizona, population of *Asterocampa celtis antonia*."

Materials and Methods

SPECIMENS:

Specimens from virtually all instars of all life stages and both sexes from each recognizable population of hackberry butterflies have been examined for characters of use in description and definition of taxa. Over 10,000 adult specimens were examined covering all known taxa from a dozen collections as listed below (Table 8). The extensive private collections of R. O. Kendall and W. J. Reinthal have also been studied.

Well over a total of 1,000 specimens of immatures stages from all taxa have been examined. Most of the latter were obtained through rearing.

Acronyms designating institutions are from Heppner and Lamas (1982).

Table 8. Institutions from which specimens were borrowed.

Acronym	**Institution**
AME	Allyn Museum of Entomology, Sarasota, Florida
AMNH	American Museum of Natural History, New York, New York
BMNH	British Museum (Natural History), London, United Kingdom*
CMP	Carnegie Museum of Natural History, Pittsburgh, Pennsylvania
FMNH	Field Museum of Natural History, Chicago, Illinois
FSCA	Florida State Collection of Arthropods, Gainesville, Florida
MNHP	Museum National d'Histoire Naturelle, Paris, France*
TAMU	Texas A&M University, College Station, Texas
UNAM	Universidad Nacional Autonoma de Mexico, Mexico, Mexico
USNM	National Museum of Natural History, Washington, D. C.
ZMHU	Zoologisches Museum, Humboldt Universität, Berlin, Germany (DDR)

*correspondence about specimens

Whereas adult butterfly specimens can be found in great numbers among museums and private collections, specimens of immature stages are few and scattered. It was therefore necessary to collect immature stages for almost all of the taxa in this study. Most of the individual specimens of immature stages examined were reared by the author.

NOMENCLATURE OF CHARACTERS:

Color descriptions were made from direct observation of live and preserved specimens and from color photographic slide transparencies taken of live material. Color names used in this work are those used in ordinary description compared with a standardized close approximation matched in the National Bureau of Standards color dictionary (Kelly and Judd, 1976).

Nomenclature used to describe the morphology of immature stages was taken from a variety of sources, including Kuznetsov (1967) and Razowski (1976). To describe head capsule structure and coloration in detail it was necessary to construct a new nomenclature of head horns, as no previous nomenclature existed. An attempt was made to use a terminology consistent with head capsule setal homology (Hinton, 1946) so as to permit phylogenetic analysis among caterpillars with homologous head capsule structure. This nomenclature (Fig. 1) was developed for use in the description of *A. idyja argus* (Friedlander, 1986a) and for use as a model for all apaturine nymphalids.

Terminology used in describing features of the wings of adult butterflies is illustrated in Figure 2.

CHARACTERS:

Characters used in this revision were compiled through detailed investigations of morphology, behavior and distribution of hackberry butterflies and their closest relatives. Most characters investigated in this study involved external cuticular structures examined by light and scanning electron microscopy. These were supplemented by life history and behavioral characters.

Representative specimens were disarticulated for morphological study, the procedures varying with the life stages involved. Specimens prepared for scanning electron microscopy (15-2000X) were air-dried or critical-point-dried and metal-coated for observation.

Study of adult morphology was carried out as proposed by Ehrlich (1958) and Sorensen (1980). Wing scale pigmentation patterns were investigated within the framework of Nijhout's (1978) model of developmental foci.

Rearing of individual specimens was conducted under standard conditions in the laboratory, as described in Friedlander (1986a). Eggs were kept in small, sealed plastic cups with leaves and a piece of paper toweling until larval eclosion. Larvae were reared in sealed plastic

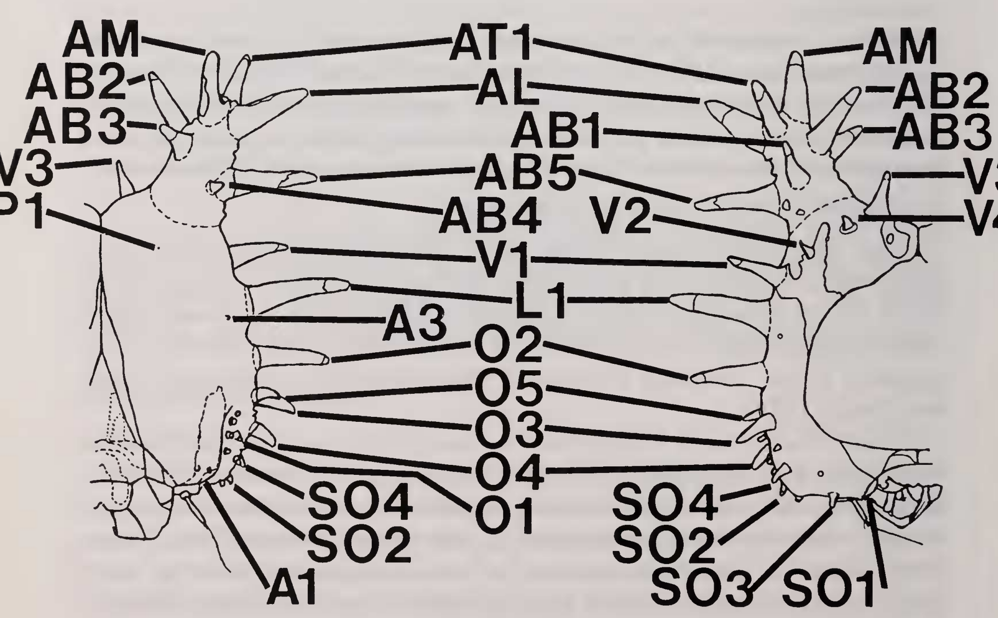

Fig. 1. Nomenclature of larval head horns (scoli).

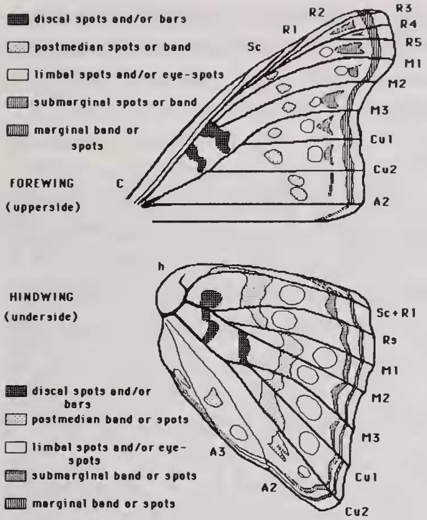

Fig. 2. Nomenclature of adult wing features (veins and markings).

bags. Fresh cuttings of suitable host plant material were provided daily or as needed. Humidity was kept high and was regulated by paper toweling, which was changed when the food was changed. Newly formed pupae were removed from rearing bags and suspended in open air cages so as to prevent damage by larvae and mold.

Behavioral data constitute an important source of characters which can best be recorded through observation in the field. Such data have previously not been applied to hackberry butterfly classification. Preliminary studies had indicated that larval and adult feeding behavior, and adult male courtship and female oviposition behaviors constituted character complexes useful in describing and defining taxa. Mating behavior constitutes one set of data which is particularly difficult to obtain. Courtships are commonly observed. Even cross-taxa couplings do occur (Ehle, 1950; A. Lewis, T. Friedlander, pers. obs.), but the success of these matings and the viability of any offspring produced is almost impossible to determine in the field.

Under artificial laboratory conditions pairings can be achieved with a minimum of effort and expense. Sleeve cages placed over fresh cuttings of the host plant exposed to normal light, temperature and humidity regimes suffice to breed hackberry butterflies. Cross-taxa pairings under these conditions can give valuable information on pre- and post-mating, potential isolating mechanisms. Combined with field data on local sympatry, cross-breeding data help indicate whether or not populations have achieved sufficient isolation between one another to warrant designating them as species relative to each other (Hafernik, 1982). A number of these crosses have been carried out, with widely varying results (see previous section on species concept in hackberry butterflies).

Distributional data include the range, dispersion and density in time characteristic of a given taxon. Correlations of such data with ecological or geological data promote hypotheses on evolutionary events leading to these observed distributional patterns.

CLASSIFICATION PROCEDURES:

Cladistic methodology (Andersen, 1978; Ashlock, 1974; Duncan and Stuessy, 1984; Estabrook, 1972; Hennig, 1966; Jong, 1980; Kavanaugh, 1972; Kiriakoff, 1959; Lundberg 1972; Wiley, 1981) was employed to construct testable hypotheses of genealogical relationships among taxa. Trees so derived were then used to infer biogeographical hypotheses about the taxa and their associated communities (Andersen, 1978; Ashlock, 1974; Cracraft, 1975; Jong, 1979; Nelson, 1974; Wiley, 1980).

Character analysis involves a 4-step process. First, homologies of characters are hypothesized (character homologies) (Atz, 1970; Bock, 1969). Multi-state characters are then investigated at the appropriate levels of universality to determine, with some associated probability, the polarity of the character states (character phylogenies) (Crisci and Stuessy, 1980; Jong, 1980; Watrous and Wheeler, 1981). Among the ways in which polarity is determined, the method of out-group comparison was used most extensively in this revision. Third, the distribution of shared, derived character states with regard to the taxa is then studied. The assignment of probabilities of their being uniquely derived is made to establish synapomorphies for tree construction (argumentation by character synapomorphies; parsimony applications). This is the basis of the cladistic method. Lastly, the correlation of synapomorphies with regard to taxa is investigated in light of the communities in which the taxa live in order to hypothesize biogeographical pathways (quasi-statistical inference by character tracks) (Eldredge and Cracraft, 1980; Felsenstein, 1982).

In this study of hackberry butterflies I also looked at Wagner networks (Lundberg, 1972).

Descriptions of *Asterocampa* Taxa

Asterocampa J. Röber 1916

Doxocopa, C. Geyer, [1828] (part)
Doxocampa, A. Seitz, 1909 (lapsus calami)
Apatura, J. B. A. Boisduval and J. E. Le Conte, [1835] (part)
Apartura, E. H. Ruffner, 1877 (part, misspelling)
Nymphalis, D. F. Poey, 1847 (part)
Chlorippe, S. H. Scudder, (1875) (part)
Chlorippus, W. T. Davis, 1924 (misspelling)
Asterocampa J. Röber, 1916; D. M. Bates, 1926 (*Apatura celtis*, type by subsequent designation)
[*Celtiphaga* W. Barnes and A. W. Lindsey, 1922 (*Apatura celtis*, type by original designation); excluded by Cowan (1970) from synonymy of *Asterocampa* by

reason of its being a junior objective synonym of *Doxocopa* Hübner through being a replacement name for *Chloripped* Doubleday]

Apatura celtis Boisduval and Le Conte was designated the type species of *Asterocampa* by Bates in 1926.

The hackberry butterflies are recognized here as forming 2 major species groups, roughly corresponding to Skinner's (1911) Celtis and Clyton species groups, respectively.

The butterflies corresponding to Skinner's Clyton group are well defined. Eggs are tightly packed in clusters by ovipositing females. These eggs have a reduced aeropylar network. Larvae feed gregariously from emergence through middle instars. Pupae have blunt head prolongations. Adults are lacking dark limbal spots on the forewings.

The butterflies corresponding to Skinner's Celtis group have fewer defining characters. They are defined in the egg stage by chorionic reticulations, in the larval stage by the reduction of the head scolus AB5 in relation to L1, and in the adult by the reduction of certain genitalic structures (length of saccus and aedeagus in male genitalia, length of ductus in female genitalia).

EGGS: The eggs of hackberry butterflies (figured in: Comstock, 1953, 1961; Edwards, 1884b, 1897; Langlois and Langlois, 1964; Pyle, 1981, 1985; Riley, 1874; Scott, 1986) are roughly spherical with a diameter of slightly less than 1 mm each, and with a flattened base and slightly flattened micropylar region. Each has from 16 to 24 slightly prominent, longitudinal (vertical), flattened ribs, which are periodically punctuated with aeropylar holes. Between adjacent ribs are fine, closely spaced, horizontal costulae which form ladder-like rows. The top of the egg is sculptured with concentric rings of polygons bounded by minute ridges. The central half dozen or more polygons form the rosette around the micropyle.

The whitish eggs are glued to the substrate with a clear mucilage which holds them in position. Eggs are usually deposited on the undersides of leaves, although females in some populations of hackberry butterflies are known to place them on uppersides preferentially, or on nearby twigs, branches or epiphytes.

Two strategies among hackberry butterflies are evidently used in oviposition. The Celtis group of taxa deposits relatively small numbers of eggs in a clutch (1-50), usually in one layer and not in a tightly packed cluster. These butterflies generally select growth points on their larval host plant as sites for oviposition. This provides early instar larvae with the newest leaves.

Females belonging to the remainder of taxa deposite eggs in larger clutches (50-500) of multilayered masses of tightly packed eggs. They place their egg masses on leaves at the ends of branches at the edges of canopies in partial sunlight. The selected host plants are generally mature trees occurring in groves.

LARVAE:

Asterocampa larvae (figured in: Boisduval and Le Conte, 1829-1833[-1837]; Comstock, 1953, 1961; Edwards, 1884b, 1897; Langlois and Langlois, 1964; Mitchell and Zim, 1964; Peterson, 1962; Pyle, 1981, 1985; Riley, 1874; Scott 1986) are fusiform and without body scoli. The body tapers anteriorly towards the laterally expanded head capsule and posteriorly towards 2 short anal horns, much like satyrine caterpillars. The head capsule bears a single, branched horn (antler) at each of the dorsolateral corners and a frill of unbranched horns along the occiput. The many body setae are borne on chalazae. Larvae are variously green and have green or brown heads marked with white. The body is striped with lines or crenations of white to yellow and is studded with the minute whitish chalazae. Overwintering larvae lose their green color and appear mottled brown to reddish brown, turning green again in the spring with resumed feeding.

Hackberry butterflies typically have 5 larval instars (Comstock, 1953; Edwards, 1884b, 1897; Riley, 1874; Friedlander, pers. obs.). The third instar is the stage that diapauses over winter (e.g., Stamp, 1983), similar to most other apaturine nymphalids (Friedrich, 1977; Osanai and Arai, 1962a, b; Shiotsu, 1977; pers. obs.).

Scott (1981a) stated that "the hibernating generation of *Asterocampa* has six instars, versus 5 for the summer generation," attributing the extra instar to a specialization for winter survival. Edwards (1882) reported six larval instars for a small percentage of individuals of the overwintering generation of one species and stated (1884c) that *A. clyton* and *A. celtis* hibernated after the third molt. In his other papers he asserted that they hibernated after the second instar. Riley (1873, 1874) remarked that larvae diapaused after passing through the second or third molt but that there were only 5 instars. He introduced the idea that the number of instars might be different for the spring and fall generations of *A. clyton* and *A. celtis*. This has not been confirmed anywhere in the literature or by personal observation (routinely only 5). Some variability in excess of 5 instars has been observed in laboratory colonies and in related genera of butterflies (e.g., Friedrich, 1977).

Larvae of the Clyton group of hackberry butterflies are intensely gregarious as early instars, feeding and resting together in large numbers on leaves. When disturbed, they relocate and reaggregate. Even as mature larvae they can be found resting side by side. Larvae of the Celtis group of Skinner, while often found together as early instars, are far less gregarious.

PUPAE:

Asterocampa pupae (figured in: Boisduval and Le Conte, 1829-1833[-1837]; Comstock, 1953, 1961; Edwards, 1884a, 1897; Langlois and Langlois, 1964; Mitchell and Zim, 1964; Mosher, 1916; Pyle, 1981, 1985; Riley, 1874; Scott, 1986) are attached to silken pads woven across the undersides of leaves (by corresponding mature larvae) by large cremasters in such a way as to hold them parallel to the leaf blades (except in *A. leilia*). The head is produced slightly into 2 horns extending beyond the eyes. The abdomen is arched and keeled dorsally, raised behind the thorax, and is laterally compressed. Pupae are also variously green and marked with whitish dots and dashes and blend in color and pattern with the leaves to which they are attached.

ADULTS:

The hackberry butterflies are medium-sized Nearctic apaturine nymphaloid butterflies. They are somewhat sexually dimorphic in size and wing shape. The males are smaller and have narrower wings. Males are most commonly encountered during their courtship, either perching on sunlit tips of branches or tree trunks or aggressively pursuing passers-by. Females are usually found in search of suitable host plants but can as often be found sunning. Both sexes are encountered at sources of adult food, such as rotting fruit.

The hindwings are always patterned with a row of submarginal dark brown spots (limbal spots) and white and brown spots usually occur on the forewings. The dark spots of the uppersides of the wings are repeated below to form eyespots with pupils. The ground color of the wings spans browns and oranges ranging from light tan to dark black. The antennae always have light-colored tips. The blue iridescence common to the Neotropical apaturine *Doxocopa* and the Palearctic *Apatura* is not found in *Asterocampa*. Structural colors occur but are ruddy and blend in with the pigments of the wings.

The genus *Asterocampa* is defined relative to other apaturine nymphaloid butterflies by its genitalia and geographic distribution. It shares with *Chitoria* larval head capsule scolar arrangement and pupal cremastral design, features which are not yet known to be shared with any other genera. Genitalia of both sexes are quite similar between *Chitoria* and *Asterocampa*. The males have a reduced gnathos and females have paired signa on the bursa. These characters have not yet been determined to be synapomorphic.

PARASITES AND PREDATORS:

The insect parasites and predators of hackberry butterflies have been reported for collections made by me through 1982 (Friedlander, 1984). The majority of these records are for individuals of the Clyton group, probably as a result of sampling frequency but possibly also as a result of the higher local density of individuals in populations of this species group.

Typical parasites of the egg stage across the genus are scelionids (Hymenoptera, Scelionidae) of the genus *Telenomus*. Their parasitism could possibly have (have had?) an effect on the egg mass design of Clyton group hackberry butterflies (Friedlander, 1986b). Trichogrammatid wasps have been found (2 per egg), but in only one collection of eggs (Celtis group).

Both hymenopterous and dipterous parasites have been reared from hackberry butterfly larvae (Diptera: Tachinidae; Hymenoptera: Braconidae, Eulophidae, Ichneumonidae). Middle instar larvae are generally attacked. All instars are attacked by both hemipteran and hymenopteran predators (Hemiptera: Pentatomidae, Reduviidae; Hymenoptera: Vespidae). With the dramatic increase in fire ant populations (*Solenopsis invicta* Buren, primarily) from Texas to Florida and northward, it is to be expected that these ants will cause heavy mortality of immature stages of hackberry butterflies across the Gulf states. Even emerging adults have been observed to be attacked by these noxious pests.

Chalcidid and ichneumonid wasps have been reared from pupae. The former is probably a primary parasite of pupae and the latter probably a larval-pupal parasite.

Adult butterflies have been observed to be attacked by both birds (sparrows) and lizards (anoles). They are often fed upon by spiders (crab spiders, house spiders, jumping spiders, orb-weavers). Occasionally a large dragonfly will take one on the wing.

ADULT BEHAVIOR:

Various aspects of adult hackberry butterfly behavior have been reviewed recently. Scott (1975, 1982 (1983)) looked at mate-locating behavior and concluded that at least 2 species of *Asterocampa* were perchers, that is, the “males rest at characteristic sites and investigate passing objects by flying out at them to search for females.” The short wings and thick bodies of males could very well be morphological adaptations to such behavior, as Scott suggests. Only one hackberry butterfly has been found to hill-top. This is *A. idyja argus* in Sonora, Mexico (D. Mullins, pers. comm.). Species of hackberry butterflies have been interpreted as being good examples for a resource-, or possibly also, female-defense polygyny mating system (Rutowski, 1984), males by their selection of perch sites monopolizing the larval host plants sought by females. This would be especially important if not only virgin females were most likely to be encountered at these sites, but also mated females capable of being mated gain.

Multiple mating does occur in *Asterocampa* (pers. obs. in field and in dissections) and males also “plug” females with a sort of sphragus, indicating that there could be an advantage for males to mate with previously mated females. Females could also benefit from multiple mating if some sort of nutrition is derived from matings.

Adult feeding behavior has been summarized by Neck (1983). Adults are attracted to a wide variety of nitrogen-rich food sources, including certain flowers.

Hackberry butterflies are for some reason often attracted to lights at night (Murtfeldt, 1884; Kendall and Glick, 1971 (1973)).

ECONOMIC IMPORTANCE:

There is very little economic literature concerning hackberry butterflies. They are occasionally recorded as pests of hackberry trees (e.g., Dodge and Rickett, 1943; Herrick, 1935) but only rarely do they cause extensive defoliation (Langlois and Langlois, 1964; Solomon *et al.*, 1975). It is interesting to note that in both cases of defoliation mentioned above, the hackberry butterfly species was *A. celtis* inhabiting an island. Both *A. celtis* and *A. clyton* are periodically very abundant across the southeastern United States where their host plants are common (Riley, 1888; Israel, 1982).

Asterocampa celtis (J. B. A. Boisduval and J. E. Le Conte, [1835])

(Genitalia, Figure 3)

Synonymies and discussion of types

Asterocampa celtis celtis (J. B. A. Boisduval and J. E. Le Conte, [1835])

?*Papilio lycaon* J. C. Fabricius, 1793 (identity obscure; junior homonym of *Papilio lycaon* Kühn, 1774)

Apatura celtis J. B. A. Biosduval and J. E. Le Conte, [1835] (biology); H. Lucas in R. de la Sagra, (1857) (Cuba!); W. H. Edwards, 1872 (biology), 1875 (biology), 1884 (biology); C. V. Riley, *et al.*, 1888 (biology); H. Edwards, 1889 (biology)

Apatura celtis aberration *alb.* H. Strecker, 1878 (abbreviated name, excluded name)

Apatura celtis alba W. G. Wright, 1905 (change of status)

Apatura alicia W. H. Edwards, 1868 (revised status)

Apatura celtis variety *alicia,* H. Strecker, 1878

Apatura herse, A. G. Butler, 1874

Apatura lycaon, A. G. Butler, 1874; C. V. Riley, 1874 (biology); M. E. Murtfeldt, 1884 (biology)

Doxocopa lycaon, S. H. Scudder, 1872

Doxocopa celtis, S. H. Scudder, 1889

Chlorippe celtis, S. H. Scudder, 1889; J. W. Tutt, 1906 (biology)

Chlorippus celtis, W. T. Davis, 1924 (misspelling)

Chlorippe celtis variety *alicia,* H. Skinner, 1911

Chlorippe celtis aberration *inornata* R. H. Wolcott, 1916 (excluded name)

Asterocampa celtis, J. Röber, 1916; W. Barnes and A. W. Lindsey, 1922 (designation of type for *Celtiphaga*); D. M. Bates, 1926 (designation of type for *Asterocampa*); W. J. Holland, 1931; J. McDunnough, 1938; H. Stichel, 1938; C. B. Williams, 1949 (biology); G. Ehle, 1950 (biology); A. B. Kots, 1951; D. L. Bauer, 1953 (biology); K. Maeki and C. L. Remington, 1960 (karyotype); P. R. Ehrlich and A. H. Ehrlich, 1961; C. F. dos Passos, 1964; T. H. Langlois and H. H. Langlois, 1964 (biology); R. Heitzman, 1965 (biology); W. H. Howe, 1975; J. D. Solomon, *et al.*, 1975 (biology); J. A. Scott, 1975 (biology), 1979 (1981) (biology); L. D. Miller and F. M. Brown, 1981, 1983; R. M. Pyle, 1981; P. A. Opler and G. O. Krizek, 1984 (biology)

Asterocampa celtis aberration *alb,* J. McDunnough, 1938 (misspelling, excluded name)

Asterocampa celtis form *alb,* L. D. Miller and F. M. Brown, 1981 (misspelling, excluded name)

Asterocampa celtis aberration *inornata,* J. McDunnough, 1938; L. D. Miller and F. M. Brown, 1981 (excluded name)

Asterocampa alicia, J. Röber, 1916; W. H. Howe, 1975 (part); L. D. Miller and F. M. Brown, 1981; R. M. Pyle, 1981 (part)
Asterocampa celtis alicia, J. McDunnough, 1938; W. D. Field, 1940 (possible partial misidentification); A. B. Klots, 1951 (part); C. F. dos Passos, 1964
Asterocampa clyton, R. M. Pyle, 1981 (probable misidentification, part: p. [49], fig. 12)
Celtiphaga celtis, W. Barnes and F. H. Benjamin, 1926
Celtiphaga celtis aberration *inornata*, W. Barnes and F. H. Benjamin, 1926 (excluded name)
Celtiphaga celtis aberration *alb*, W. Barnes and F. H. Benjamin, 1926 (misspelling, excluded name)
Celtiphaga celtis alicia, W. Barnes and F. H. Benjamin, 1926

This taxon was based on a color drawing and life history notes supplied to Le Conte by John Abbot of Georgia in 1813[-1836] (Rogers-Price, 1983). Abbot considered the butterfly rare in swamps occurring near his home (Scudder, 1872b) in Screven County, Georgia. The figures of the adult are to be considered as representing the type. The description of this species, and thus the nominate subspecies, is considered to be complete in [1835] with the publication of the plate (Cowan, 1970). The whole description of *Apatura celtis* was complete in [1837].

Apatura alicia Edwards is based on 2 female specimens supplied to W. H. Edwards by E. Norton from the vicinity of New Orleans. Neither specimen could be located in Edwards' collection or elsewhere and so the beautiful and accurate figures published by him in the original description serve to represent the types. This taxon is considered here to be a subjective synonym of *A. celtis celtis*. It is a Gulf coast population of *A. celtis celtis* showing some differentiation but blending by degrees inland. The name has long been mistakenly used for populations of *A. celtis* in peninsular Florida (e.g., Edwards, 1880a-c) but must remain tied to butterflies of Louisiana and neighboring states. As a result, much of the argumentation as to its distinctness has been misapplied.

Apatura celtis alba Wright became available for synonymy in 1905, and is a name given to a color form of *Asterocampa celtis celtis*. The type is represented in W. H. Edwards (1875), figure 5 of *Apatura celtis*. By implication its type locality is Coalburgh, West Virginia.

***Asterocampa celtis reinthali*, New Subspecies**

?*Papilio lycaon* J. C. Fabricius, 1793 (identity obscure; junior homonym of *Papilio lycaon* Kühn, 1774)
Apatura alicia, W. H. Edwards, 1880 (biology); H. Edwards, 1889 (biology)
Chlorippe alicia, W. J. Holland, 1898
Asterocampa alicia, W. J. Holland, 1931; W. H. Howe, 1975 (part); R. M. Pyle, 1981 (part); P. A. Opler and G. O. Krizek, 1984 (clinal subspecies?)
Asterocampa celtis alicia, W. M. Davidson, 1958 (biology); A. B. Klots, 1951 (part)

This taxon, named after the late Dr. Walfried J. Reinthal, has previously been included under the name *Asterocampa alicia*. Like *A. alicia*, it is a large, coastal *A. celtis*. The male type is selected from specimens taken in April at Ocoee, Florida ("A. alicia, 4-5-39. Ocoee, Fla." "collected by, Mrs. C. N. Grimshawe, Miami, Florida"). The female allotype ("A. alicia, 4-7-49, Ocoee, Fla" "collected by, Mrs. C. N. Grimshawe, Miami, Florida") will be deposited with the holotype at the Carnegie Museum of Natural History.

The types are selected from a series of specimens set aside by Dr. Reinthal in his own collection. The remaining 10 specimens in this series are designated paratypes. All will be deposited in the Carnegie Museum of Natural History.

Paratype males (5): "Largo, Fla, VII-11 '49, F. H. C." "W. J. R."; "Port Orange, Fla. 7-17-48" "A. celtis alicia [male]" "W. J. R."; "FLA: Orange Co., Ocoee. 11-12.vi.1954, J. Bauer, C. M. Acc. 17023" "21.vi." "W. J. R.", 16.VII.49, Largo, Fla, F. H. C. "; "13.IV.57, Oviedo, Fla, [male] alicia" "Genit. prepar., No 17 1959, W. J. Reinthal" [no head, no abdomen].

Paratype females (5): "Lk. Okeechobee, Fla. VII-21-1940" "F. H. Chermock, Coll." "W. J. R. " [no abdomen]; "Fla. St. Johns Co., Summer Haven 16 mi., St. Augustine, E. P. Mellon II 3 VIII 1953" "W. J. R."; "19.VIII.37, Ocoee, Fla, A. alicia"; "16.VII.49, Largo, Fla, F. H. C." [no head, no abdomen]; "5.VIII.56, Oviedo, Seminole Co., Fla." "Genit. prepar., No 18 1959, W. J. Reinthal" [no head, no abdomen].

Asterocampa celtis antonia (W. H. Edwards, [1878])

Apatura antonia W. H. Edwards, 1877 [1878]; F. M. Brown, 1967 (lectotype, type locality)
Apatura celtis variety *antonia*, H. Strecker, 1878
Apatura celtis variety *antonio*, J. B. Smith, (1884) (misspelling)
Apatura celtis, E. M. Aaron and S. F. Aaron, (1885) (part)
Apartura celtis, E. H. Ruffner, 1877 (part, misspelling)
Apatura antonia variety *montis* W. H. Edwards, 1883; W. G. Wright, 1905, C. J. Maynard, 1891 (revised status)
Apatura montis, W. G. Wright, 1905; B. N. Schwanwitsch, 1924 (morphology); F. M. Brown, 1967 (lectotype)
Chlorippe antonia, W. J. Holland, 1898
Chlorippe montis, W. J. Holland, 1898
Chlorippe leilia, W. J. Holland, 1898 (misidentification)
Chlorippe antonia montis H. G. Dyar, [1903]
Chlorippe celtis variety *antonia*, H. Skinner, 1911
Chlorippe celtis variety *montis*, H. Skinner, 1911; V. F. Calkins, 1932
Doxocopa celtis, F. D. Godman, (1901) (part)
Doxocopa antonio, K. R. Coolidge, 1911 (misspelling)
Doxocopa montis, K. R. Coolidge, 1911
Doxocopa leilia, K. R. Coolidge, 1911
Asterocampa leilia antonia, J. Röber, 1916; H. Stichel, 1938

Asterocampa leilia, W. J. Holland, 1931 (misidentification); J. S. Garth, 1950 (misidentification); R. M. Pyle, 1981 (misidentification, part: p. [284]); P. M. Montgomery, 1984 (misidentification: p. 4)
Asterocampa celtis antonia, J. McDunnough, 1938; A. B. Klots, 1951; C. F. dos Passos, 1964; K. S. Brown, Jr., 1965
Asterocampa celtis montis, J. Röber, 1916; J. McDunnough, 1938; H. Stichel, 1938; A. B. Klots, 1951; C. F. dos Passos, 1964
Asterocampa celtis, C. C. Hoffmann, 1940 (part); P. R. Ehrlich and A. H. Ehrlich, 1961 (part); J. A. Scott and G. R. Scott, (1980) (part, biology); R. M. Pyle, 1981 (misidentification, part: p. [285])
Asterocampa antonia, W. J. Holland, 1931; W. J. Reinthal, 1966 (biology); W. H. Howe, 1975; L. D. Miller and F. M. Brown, 1981, 1983; R. M. Pyle, 1981
Asterocampa antonio, E. R. Tinkham, 1944 (misspelling)
Asterocampa montis, W. J. Holland, 1931; W. H. Howe, 1975; L. D. Miller and F. M. Brown, 1981, 1983; R. M. Pyle, 1981
Asterocampa subpallida, J. A. Comstock, 1953 (possible misidentification, part: p. 134)
Celtiphaga celtis antonia, W. Barnes and F. H. Benjamin, 1926
Celtiphaga celtis montis, W. Barnes and F. H. Benjamin, 1926

Apatura antonia Edwards (1877 [1878]) was described from a series of specimens taken in Texas by J. Boll and G. W. Belfrage of Texas (and a collector in Arizona, possibly Dr. Charles Smart (Brown, 1967)). The type locality is restricted by F. M. Brown (1967) and a lectotype was designated by him and W. J. Reinthal in the same article. The type and paratypes have been examined and are in the Carnegie Museum of Natural History.

Edwards (1883) characterized *A. antonia* variety *montis* after receiving a series of specimens collected by H. K. Morrison from Arizona. He compared these with his collection of *A. antonia*-like specimens which included specimens from J. Doll (Arizona, *etc*?) and E. A. Dodge (Colorado). Brown (1967) selected the lectotype, which together with paratypes are deposited in the Carnegie Museum of Natural History. These also have been examined.

A good discussion of Edwards' type material is found in Brown (1967).

Diagnoses of taxa

A. celtis is a member of the Celtis group. Virtually all larvae of *A. celtis celtis* lack the antler scoli AB5. Adults are best distinguished by the single, large unpupilled eyespot of the forewing (Cu1). Limbal spot M3 above it is usually small and may be ringed posterobasally with dark brown and orange. It is virtually impossible to separate individuals of *A. celtis antonia* and *A. celtis celtis* in hybrid zones. As a rule of thumb, specimens with equal-sized spots M3 and Cu1 can be assigned to *A. celtis celtis* if the former spot is entirely white. Populations exhibiting intermediate coloration and pattern extend from northwestern Nebraska to central Texas. Similar difficulties are encountered in separating *A. celtis celtis* from *A. celtis reinthali* in zones of presumed hybridization in northern Florida and coastal Georgia and South Carolina.

The whitish yellow larval markings of *A. celtis reinthali* are much more yellow than in *A. celtis celtis*. The supraspiracular markings tend to be obscure rather than to form a crenated line. Mature larvae are known to have well developed antler scoli AB5 like those found in *A. celtis antonia*, but which are virtually absent in *A. celtis celtis*. Adult *A. celtis reinthali* are considerably larger than the nominate subspecies, and have a brighter ground color above and larger, lighter blue pupils in the ocelli. The pupils of Cu1 in the FW above are lateral (off-center) and the limbal spots M1 of the HW are asymmetrical, each being drawn out into a point distally, and their pupils with scales dividing in 2 tracks outwardly. The butterflies are peninsular Floridian in origin. They differ from true *A. alicia* (here, *A. celtis celtis* form "alicia") not so much in size but in coloration and pattern. True *A. alicia* is darker in ground color (grayish brown), the pupils of eyespots are smaller, and limbal spots Rs of the HW are not drawn out into points laterally.

A. celtis antonia is more western than the other two and differs from them in the adult stage by retaining eyespots in the FW. These limbal spots are not generally expressed in the other subspecies. The host plant most commonly used is *Celtis reticulata* Torrey. Larvae differ by retaining all the antler scoli AB5 commonly being lost in the eastern subspecies.

Descriptions of life stages

Immature stages of *A. celtis celtis* were described in detail by Riley (1874), Edwards (1875, 1880c, 1884b) and Scudder (1889). Those of *A. celtis reinthali* were described in detail by Edwards (1880c). Immature stages of *A. celtis antonia* are described here for first time. Pyle (1984) describes the rearing of this species in Colorado in his popular account of butterfly natural history. Scott (1986) illustrates eggs of *A. celtis celtis* in an excellent color photograph (Pl.1, [fig.] 140). Pyle (1981, 1985) photographically illustrates the mature larva and pupa of *A. celtis celtis* (Pl. 45R, 45L).

EGGS AND EGG DEPOSITION:

Eggs of *A. celtis celtis* finely sculptured with reticulations between costae, except in micropylar region, 16-21 ribs; 0.7-0.9 mm wide, 0.9 mm high. Micropylar rosette with 9 petals.

Light yellow eggs of *A. celtis reinthali* deposited in small clusters on undersides of leaves or on branches and epiphytes on larval host plant *Celtis laevigata* Willd. Other details of egg morphology expected to be quite similar to those of *A. celtis celtis*. Edwards (1880c) reported pale yellow-green eggs having 20 vertical ribs.

Eggs of *A. celtis antonia* finely sculptured, slightly reticulated between costae, with 17-24 ribs; those from southeastern part of range with fewer ribs than those from far western limits. Dimensions 0.8-0.1 mm wide, 0.8-1 mm high. Micropylar rosette with 11-14 petals.

LARVAE:

First instar head capsule of *A. celtis celtis* very dark brown, with 5 pairs of scoli developed, scoli almost twice size of simple eye; 0.63-0.74 mm wide. Body length about 3.5 mm. Head and proleg setae unbranched; body setae extremely short-branched. Crampets (Pl.17, fig. C; defined in: Friedlander, 1986a) present on prolegs. Mandibles with teeth. Body light green. Anal horns about 0.1 mm long each, light brown. First instar larval head capsule of *A. celtis reinthali* dark brown. Body green; total length about 2 mm. First instar larva of *A. celtis antonia* with dark brown head capsule, scoli twice width of simple eye. Anal horns developed.

Second instar larva of *A. celtis celtis* with long scoli, antlers somewhat lateralized (diverging at nearly a right angle), AB5 absent. Head capsule very dark brown. Scoli V2 absent. Whitish body markings obvious in this stage. Anal horns green, variably sclerotized. Head capsules of second instar larva of *A. celtis reinthali* very dark brown, rarely green with brown antlers, AB5 absent, antlers lateralized. Body green with whitish lines and crenations as in mature larva. Total length about 3.5 mm. Head capsule of second instar larva of *A. celtis antonia* mostly dark brown. Scoli AL spine-like, antler base less than mandibular width, AB5 about half as long as L1. Scoli V2 absent, Anal horns tan.

Third instar head capsule of *A. celtis celtis* mostly dark brown. Body coloration as in second instar. Third instar larva of *A. celtis reinthali* with variably dark brown to mottled head capsule, with somewhat lateralized antlers. Body green with markings as before; total length about 7.5 mm. Third instar larva of *A. celtis antonia* with mostly dark brown head capsule. Diapausing larvae with reduced antlers (shorter with less well developed scoli), body with mixed gray, brown and pink.

Fourth instar of *A. celtis celtis* with head capsules mostly brown. Body markings same as mature larva. Fourth instar larva of *A. celtis reinthali* also with head capsule variably brown. AB5 small to vestigial. Body same as third instar, except heart-line spots apparent. Total length about 14 mm. Fourth and fifth instar larvae of *A. celtis antonia* in 2 color morphs with regard to head capsule: brown (brown striped; most of head capsule dark brown); green (at extreme, only antlers brown).

Fifth instar larva of *A. celtis celtis* green. Head capsule either green or dark brown with lateral whitish streaks, antlers always with black tips. Heart-line with yellowish white spots anteriorly on abdominal segments, broadened into chevrons into inner subdorsal band region. Dorsolateral stripe yellowish white. Crenated line of yellowish white in supraspiracular area, sometimes broken into dashes. Subspiracular stripe whitish. Anal horns long. Total length about 30 mm.

Fifth instar larva of *A. celtis reinthali* green, with variably colored head capsule, green to dark reddish brown, with whitish vertical stripes laterally, and black-tipped antlers. Heart-line marked with small yellow spots. Dorsolateral and subspiracular stripes yellowish. Supraspiracular area marked with diagonal dashes of yellowish white, higher ends posteriorly. Anal horns long. Body markings somewhat obscure compared to earlier instars. Length of males about 29 mm, females, 36 mm.

Fifth instar larval head capsule of *A. celtis antonia* with long antlers, 1.7 mm, not including terminal scoli. AL and AM subequal, of moderate length, slightly smaller than AB2 and AB5. AB1, AT1, AB3 and AB4 (in order) even smaller. L1 longest of head scoli, 0.9 mm, followed by O2, V1, V3 and O3. Ratio of AB5 to L1 approximately 0.6. Head capsule 3.2 mm high, excluding mandibles. Mandible with one notch in incisor. Body color green. Heart-line with yellowish white spots anteriorly on middle abdominal segments; lacking in form called here "mexicana" (see: adult description). Dorsolateral stripe yellowish white to light yellow, somewhat wavy in some populations. Subdorsolateral and supraspiracular areas with diagonal yellowish white dashes, posterior ends higher, connecting with posterior vertical bar, almost connected below bar by chalazae to form crenated line (with ascending bars); obscure in "mexicana." Subspiracular stripe yellowish white. Shade of green and amount of yellowish in both body color and in stripes varies.

PUPAE:

Pupa of *A celtis celtis* 19-25 mm long, about 8-9 mm high at abdominal crest maximum. Head prolongations elongate, pointed. Body light green, finely speckled with light yellow or whitish dots, marked with yellowish white along dorsal crest, wing veins and wings' edges posteriorly. Supraspiracular transverse dashes present; subspiracular line an extension of one along the outer wing margin, almost forming an undulating line. Crest finely serrate, with blunt spines anteriorly on each segment subtended by pair of small black spots. Pupal cremaster length 2.3-2.8 mm. Length of pupa of *A. celtis reinthali* 23-25 mm, width about 8 mm, maximum height about 10 mm. Head prolongations prominent, pointed. Body yellowish green, speckled with yellowish white dots, marked with pale yellow and whitish streaks. Streaks along dorsal crest from head prolongations, merging on thorax; also posteriorly down serrated abdominal portion. Both wing veins and posterior wing edges so marked. Indications of supraspiracular transverse dashes present. Abdominal crest with blunt spines anteriorly on each segment subtended by pair of small black dots. Pupa with cremastral length of 2.5-2.9 mm. Pupa of *A. celtis antonia* green, usually speckled with white, with whitish markings along dorsal crest, wing veins and margins, and in diagonal streaks on sides of abdomen. Length 17-21 mm, height at crest maximum 6.5-9.0 mm. Head prolongations sharp. Some development of eye spines, as in *A. leilia*, as best seen in form "mexicana." Abdominal crest finely serrate, anterior margins of segments blunt-spined with subtending small black dots, one on each side. Subspiracular line on abdomen usually present. Pupal cremaster length 2.3-2.8 mm. Pupal cases with greenish cast after emergence, whitish markings apparent.

ADULTS:

Antennae of *Asterocampa celtis celtis* (Pl.20, figs. A-C) dark brown, finely ringed with lighter brown on flagellar segments giving faintly dotted appearance; apical portions slightly swollen, dark brown with bare pale yellow (tan with aging of preserved specimens) tips. Palps, general body scaling and ground color of wings above, grayish brown and yellow orange mixed. Forewing costal length (Figure 4) of *A. celtis celtis* 20.0-28.5 mm (males, 24.0 ± 1.6 mm, n = 248), 22.0-32.5 mm (females, 27.3 ± 1.8 mm, n = 151); larger, coastal form "alicia" accounts for most of high values in both sexes. Male genitalia: saccus 2.2-

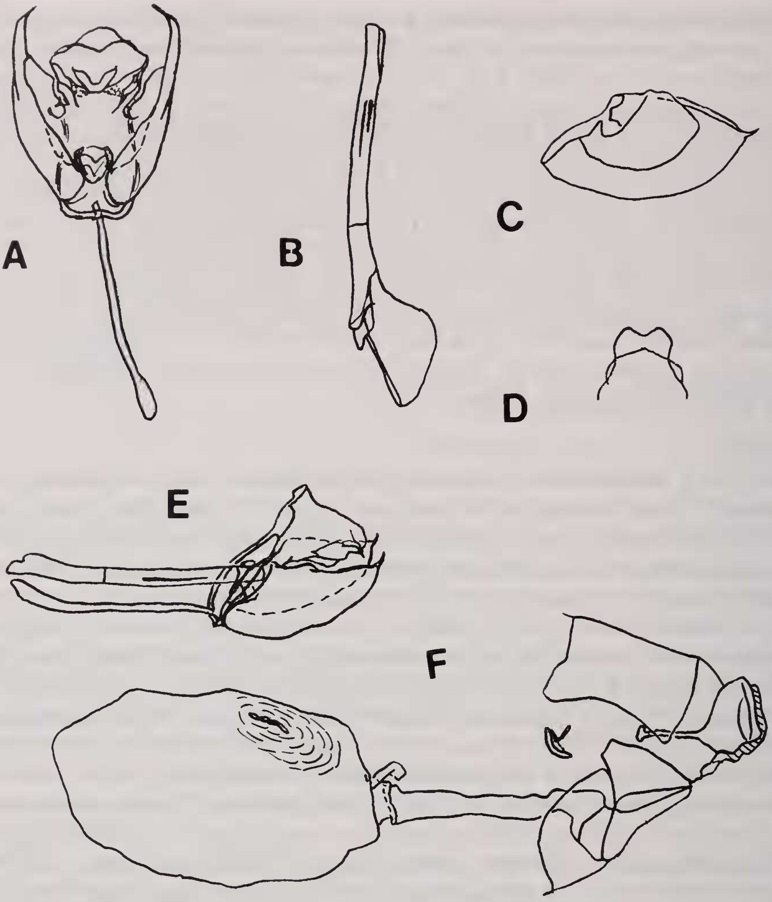

Fig. 3. Genitalia of *Asterocampa celtis* (B. & L.).
Male genitalia
Whole genitalia (**A**, ventral view, valves spread) with aedeagus (**B**) separate: Texas: Travis Co., Austin, September 1977, t. Friedlander. TF gen. prep. no. 1977. *A. celtis antonia* (Edwards).
Right valve (**C**, mesal view) and uncus (**D**, ventral view): Louisiana, no date, CMNH. TF gen. prep. no. 1982–30. *A. celtis celtis*.
Whole genitalia (**E**, left lateral view): Texas: Travis Co., Austin, September 1977, T. Friedlander. TF gen. prep. no. 1977. *A. celtis antonia.*
Female genitalia:
Whole genitalia (**F**, left lateral view): Texas: Travis Co., Austin, September 1977, T. Friedlander. TF gen. prep. no. 1977. *A. celtis antonia.*

2 6 mm, aedeagus 2.9-3.2 mm, valves 1.9-2.2 mm, uncus shallowly bifid, hairs of anal brush recurved. Female genitalia: ductus 1.7-2.4 mm, signa on elongate corpus 2 long longitudinal strips on right side. For a more complete description of this subspecies the reader should consult my dissertation.

Photographic figures of *A. celtis celtis* found in: Ebner, 1970 (p. 95, male, d, v); Harris, 1972 (Plate 6: fig. 1, male, d; fig. 2, female, d); Holland, 1898, 1931 (Plate

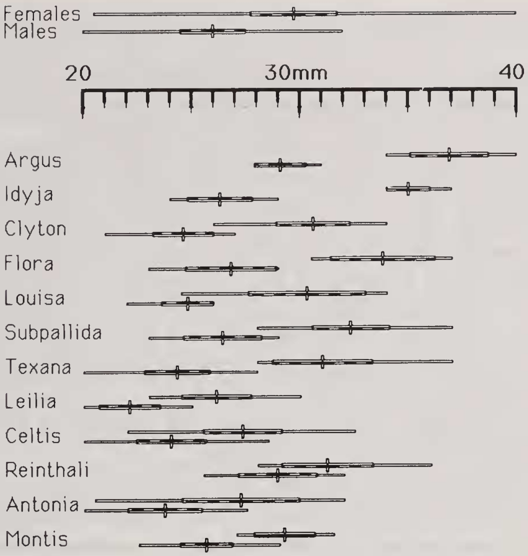

Fig. 4. Costal forewing measurements of hackberry butterflies, showing mean lengths, ranges and one standard deviation, given in millimeters.

XXIII: fig. 3, male, d; fig. 4, female, d; fig. 13, male, v); Milne and Milne, 1980 (Plate 604, male, d); Opler and Krizek, 1984 (Fig. 191, male, d; Fig. 192, male, v); Pyle, 1981 (Plate 664R, male, d); Pyle, 1985 (Plate 664L, male, v; Plate 664R, male, d); Scott, 1986 (Plate 22 [fig.] 140, female, d); Smart, 1977 (p. 210, fig. 8, male, d); Sutton and Sutton, 1985 (Plate 366, males, v.d); Williamson, 1979 (cover photograph. v); Wright, 1906 (Plate XXIII: fig. 245, female, d). Howe (1975) illustrated individual specimens (Plate 11: fig. 11, female, d; fig. 12, male, d; fig. 25, male, v).

A. celtis celtis dorsal FW limbal spots mostly white. Spot M1 usually white, but sometimes mostly white with dark brown basally. Spot Cu1 dark brown, usually larger than M1 and noticeably the largest limbal spot, surrounded by yellowish orange ring (more organe in "alicia"). Spot Cu2 sometimes faintly indicated by dark brown spot with blush of yellowish orange scaling anterobasally. Limbal spots of dorsal HW large (Sc+R1 to Cu2), dark brown in local field (merging rings) of yellow orange in orange.

Ventrally, FW limbal spots R5, M2 and M3 white. Spot M1 basally dark brown, apically white, ringed in light yellow (yellow more intense in "alicia"). Spot Cu1 large, dark brown, ringed in light yellow, without pupil. Limbal spots of ventral HW (Sc+R1 to A2) dark brown with whitish blue pupils, ringed in yellow in local brown ring in tan field. Spot A1 joined to Cu2 at inner dark brown scaling, or vestigial. Spot A2 without pupil and outward brown ring, usually small, oval.

Antennae of *Asterocampa celtis reinthali* (Pl.20, figs. D-F) like those of *A. celtis celtis*. Palps, general body scaling and ground color of wings above, grayish brown and burnt orange mixed. Costal lengths of forewings (Fig. 4) of *A. celtis reinthali*, 25.5-32 mm (males, 28.9 ± 1.8 mm, n = 44), 28-36 mm (females, 31.2 ±

2.1 mm, n = 26). Male genitalia similar to *A. celtis celtis*: saccus 2.8-3.0 mm, aedeagus 3.6-4.3 mm, valves 2.0-2.5 mm, uncus shallowly notched, dorsal brush with upwardly curved hair-scales. Female genitalia: ductus 2.4-2.6 mm, signa 2 long strips on right side of elongate bursa. For a more complete description of this subspecies the reader should consult my dissertation.

Photographic illustration of adult of *A. celtis reinthali* found in: Harris, 1972 (Plate 6: fig. 3, male, d; fig. 4, female, d); Holland, 1898, 1931 (Plate XXIII: fig. 9, male, d; fig. 10, female, d); Lewis, 1973 (p. 13: fig. 6, male, d); Scott, 1986 (Plate 19 [fig.] 140d, male, d). Excellent drawings made by Howe (1975) of individual specimens (Plate 11: fig. 9, male, v; fig. 23, female, d; fig. 24, male, d).

A. celtis reinthali dorsal FW limbal spots mostly white. Spot M1 basally dark brown. Spot Cu1 noticeably the largest limbal spot, dark brown with small lateral pupil, surrounded by orange ring. Limbal spots of dorsal HW (Rs to Cu2), dark brown, sometimes with bluish white pupils, in orange field. Spot M1 usually elongated laterally. Limbal spots of HW dorsally in females in field of light yellow orange in larger field of orange.

Ventrally, FW limbal spots R5, M2 and M3 white. Spot M1 dark brown basally, white apically, ringed in yelllow. Spot Cu1 dark brown with yellow ring (orange brown at junction) with a few bluish white scales forming pupil. Limbal spots of ventral HW (Sc+R1 to Cu2) dark brown with large whitish blue pupils, ringed in strong yellow-orange in local dark brown field. Spot M1 asymmetrically elongate, pointed basally with scales of pupil merging distally. Spot A1 joined to Cu2, often vestigial. Spot A2 dark brown with strong yellow-orange ring, elongate.

Antennae of *Asterocampa celtis antonia* (Pl.20, figs, G-O) dark brown, finely ringed with lighter brown on flagellar segments giving decidedly dotted appearance; apical portions as before, except club relatively shorter. Palps, general body scaling and ground color of wings above, medium brown (more orange in some populations) and dark brown mixed. Postmedian spots of ventral HW prominent to obscure. Eastern forms with forewing costal length 20.0-27.5 mm (males, 23.7 ± 1.7 mm, n = 182), 20.5-32.0 mm (females, 27.2 ± 2.7 mm, n = 123). Form "mexicana", found in the lower Rio Grande valley of Texas and southward with small females, accounts for most low values. Western form "montis" slightly larger, 22.5-29.0 mm (males, 25.6 ± 1.2 mm, n = 89), 27.0-31.5 mm (females, 29.2 ± 1.4 mm, n = 16). Male genitalia: saccus 1.9-2.3 mm, aedeagus 2.5-3.0 mm, valves 1.5-1.9 mm. Uncus with shallow notch. Dorsal brush with upturned hair-scales. Female genitalia with short ductus (1.5-2.2 mm), bursa globular, often with 2 sclerotized signa, in longitudinal strips of right side. For a more complete description of this subspecies the reader should consult my dissertation.

Photographs of adult of *A. celtis antonia* published in sources: Brown, 1967 (Fig. 18, antonia, lectotype, male, d, v; Fig. 19, montis, lectotype, male, d, v); Ferris and Brown, 1981 (p. 356, antonia, male, d, v); Holland, 1898, 1931 (Plate XXIII: fig. 7, near antonia, male, d; fig. 8, near antonia, female, d; fig. 11, montis, male, d; fig. 12, antonia, male, d); Montgomery, 1984 (p. 4, "Empress Leilia . . . ," male, d); Pyle, 1981 (Plate 662R, mexicana, female, d; Plate 663L, antonia, male, v; Plate 664L, antonia, male, v); Pyle, 1985 (Plate 663L, antonia, male, v; Plate 663R, mexicana, female, d); Scott, 1986 (Plate 19 [figs.] 140, male, d; 140b, female, d; 140c, male, v). Excellent figures of individual specimens found in Howe (1975: Plate 11: fig. 21, near antonia, female, d; fig. 22, near antonia, male, d; Plate 12: fig. 11, antonia, male, d. v; fig. 12, antonia, female, d. v; Plate 13: fig. 6, montis, male, d, v; fig. 7, montis, female, d, v).

A. celtis antonia dorsal FW limbal spot R5 white, large. Spot M1 white with dark brown basal cup or, more typically, entirely very dark brown with white pupil, usually small. Spot M2 white, medium-sized, sometimes bordered anterobasally with dark brown. Spots M3 and Cu1, large, subequal in size, very dark brown with white pupils, ringed with light brown. Spot Cu1 in "montis" pupilled with bluish white scales, laterally. Rarely, spot Cu2 indicated by tiny, very dark brown spot. Limbal spots of dorsal HW large (Sc+R1 to Cu2), very dark brown, last few pupilled with bluish white to white, all in field of ground color, or, especially in females, in field of a more yellowish brown.

Ventrally, FW limbal spots M1, (rarely M2), M3, and Cu1 very dark brown with pupils of light blue to white, all surrounded by local field of yellow inside dark brown rings. Spot R5 sometimes expressed as eye-spot in males. Spot M2 most often white with border of dark brown and yellow anterobasally, but full range of expression occurs. Limbal spots of ventral HW (Sc+R1 to A2) very dark brown with whitish blue pupils, also surrounded by local field of yellow inside dark brown rings.

Range

A. celtis celtis (Pl.1): Eastern United States and extreme southern Ontario, Canada. Specimens examined (over 1,500 non-reared adults; state localities given alphabetically by counties):

CANADA: Ontario (province)

U.S.A.: ALABAMA: Elmore, Greene, Jackson, Madison, Marengo, Mobile, Montgomery, Tuscaloosa; ARKANSAS: Desha, Faulkner, Hempstead, Jefferson, Pulaski, Sharp, Washington; COLORADO: Denver, Jefferson, Yuma; CONNECTICUT: Fairfield, Litchfield, New Haven, Tolland; FLORIDA: Leon, Liberty; GEORGIA: Bibb, Chattahoochee, Clarke, Decatur, De Kalb, Monroe, Walker; ILLINOIS: Adams, Cook, Logan, Macon, Madison, Mercer, Platt; INDIANA: Adams, Carroll, Jackson, Knox, Kosiusko, Marion, Vigo, Wabash; IOWA: Dallas, Fremont, Polk, Pottawattamie; KANSAS: Cherokee, Douglas, Franklin, Greenwood, Johnson, Labette, Shawnee, Sumner, Wyandotte; KENTUCKY: Jefferson; LOUISIANA: East Baton Rouge, Jefferson, Jefferson Davis, Rapides, Sabine, St. Charles, St. Landry, St. John The Baptist (parishes); MARYLAND: Allegany, Baltimore, Washington; MASSACHUSETTS: Hampshire; MICHIGAN: Washtenaw; MINNESOTA: Clay, Faribault, Hennepin, Ramsey; MISSISSIPPI: Clay, Grenada, Hancock, Hinds, Lee, Lowndes, Madison, Oktibbeha, Rankin, Simpson, Tallahatchie, Tippah, Warren, Wilkinson; MISSOURI: Clay, Cole, Jackson, Jasper, Laclede, Pike, St. Louis; NEBRASKA: Adams, Cherry, Douglas, Lancaster, Platte, Red Willow; NEW JERSEY: Bergen, Essex, Middlesex, Morris, Sussex; NEW YORK: Columbia, Greene, Richmond (Staten Island), Tompkins, Westchester; NORTH CAROLINA: Cabarrus, Durham, Halifax, Mecklenburg, Orange; OHIO: Erie, Franklin, Hamilton, Miami, Montgomery, Pike; OKLAHOMA: Cleveland, Cotton, Garfield, Mayes, McCurtain, Murray, Oklahoma, Osage; PENNSYLVANIA: Allegheny, Beaver, Berks, Bucks, Franklin, Greene, Lancaster, Lycoming, Washington, Westmoreland; SOUTH CAROLINA: Calhoun, Charleston, Edgefield, Pickens, Richland; SOUTH DAKOTA: Brookings, Grant, Roberts; TENNESSEE:

Anderson, Davidson, Giles, Knox, Madison, Marion, Maury, Polk, Sullivan, Wilson; TEXAS: Bastrop, Bowie, Brazos, Dallas, Denton, Harris, Harrison, Houston, Kaufman, Limestone, Tarrant, Travis, Van Zandt, Williamson; VIRGINIA: Bath, Essex, Fairfax, Fauquier, Loudoun, Montgomery, New Kent, Washington, Wise; WASHINGTON, D. C.; WEST VIRGINIA: Hampshire, Kanawha, Morgan; WISCONSIN: Oneida.

A specimen captured in Montreal, Quebec, Canada (Stevenson, 1899) is to be considered a stray and most probably was an importation.

A. celtis reinthali: Peninsular Florida, coastal Georgia and South Carolina. Specimens examined (over 350 non-reared adults):

U.S.A.: FLORIDA: Alachua, Brevard, Flagler, Hernando, Indian River, Nassau, Okeechobee, Orange, Palm Beach, Pinellas, Polk, Sarasota, St. Johns, Seminole, Volusia; GEORGIA: Camden, Chatham, Glynn, Liberty, McIntosh; SOUTH CAROLINA: Charleston, Jasper.

A. celtis antonia: Northern Mexico, southwestern United States: Arizona, western Colorado, western Kansas, western Nebraska, New Mexico, western Oklahoma, western Texas; rarely, southern California (San Bernardino County), southern Nevada and Utah; forming hybrid zone with *A. celtis celtis* from Texas to Nebraska. Specimens examined (over 1000 non-reared adults) [from "montis" (°) (over 250 non-reared adults)]:

MEXICO: Chihuahua, Hidalgo, Nuevo Leon, San Luis Potosi, Tamaulipas [states]

U.S.A.: ARIZONA°: Cochise, Coconino, Gila, Graham, Pima, Pinal, Santa Cruz, Yavapai; COLORADO: Boulder, Clear Creek, Denver, Douglas, Jefferson, Yuma; KANSAS: Shawnee, Summer; NEBRASKA: Dawes, Sioux; NEW MEXICO: Bernalillo, Catron°, Dona Ana°, Eddy, Grant°, Luna, Otero°, San Miguel, Sierra°, Socorro°, Union; OKLAHOMA: Blaine, Caddo, Catton, Garfield, Kiowa, Lawton, Woodward; TEXAS: Armstrong, Bailey, Baylor, Bee, Bell, Bexar, Blanco, Bosque, Brewster°, Brisco, Brooks, Caldwell, Calhoun, Cameron, Coleman, Collingsworth, Comal, Crockett, Dallas, Duval, Frio, Gillespie, Gonzales, Hall, Hays, Hidalgo, Jeff Davis°, Jones, Kenney, Kerr, Kleberg, Live Oak, Llano, Lubbock, Mason, McCulloch, McLennan, Medina, Mitchell, Nueces, Palo Pinto, Pecos, Presidio, Randall, San Patricio, Shackelford, Starr, Sterling, Sutton, Tarrant, Terrell, Tom Green, Travis, Val Verde, Webb, Wheeler, Wichita, Wilbarger; also, rarely: Bastrop, Caldwell, Coryell, Lee, Parker; UTAH°: Weber [dubious record], Washington; WYOMING: Laramie.

A. celtis antonia occurs in Garfield county, Utah (Callaghan and Tidwell, 1971 (1973)) and is expected to be found in 4 more of the southern counties (Gillette, 1983). Unpublished records are available for Grand, San Juan and Washington counties, Utah (Gilette, pers. comm.). Garth's (1950) record of *A. leilia* from the Grand Canyon (Arizona) is also this subspecies of *A. celtis*. John Emmel (in correspondence) gives one record of this butterfly from the San Bernardino Mts. in southern California, tentatively considered a stray.

Discussion

A. celtis celtis is a common woodland butterfly and is perhaps the best known of the hackberry butterflies. Its colonizing ability exceeds that of

A. clyton and it is to be expected to be found beyond the range of its host as a stray. It will probably be found extending its range northwestward towards Montana as hackberry trees are planted there as windbreaks.

A. celtis reinthali is the large *A. celtis celtis*-like butterfly of peninsular Florida and the southern Atlantic coast. This subspecies was long included under the name of *A. alicia* but the two have been known for the last 30 years to be different. It probably evolved through isolation in central Florida during the glacial maxima of the Pleistocene. It is currently hybridizing on both the Gulf and Atlantic coasts.

These butterflies are similar to *Papilio lycaon* Fabricius, which was based on a drawing of a butterfly from the collection of D. Drury. F.M. Brown (1965) has shown that butterflies in Drury's collection included those from the southeastern United States. It remains possible that *Papilio lycaon* Fabricius was a hackberry butterfly.

Lucas' (1857) record of *A. celtis* occurring in Cuba should be seriously considered. It is possible that this species could have been (or still could be) on the island. If so, I think that the subspecies in question would more likely have been (be) *A. celtis reinthali* than *A. celtis antonia.*

A. celtis antonia is often confused with *A. leilia.* Holland (1898, 1931) published a photograph of *A. montis* mistakenly under the name of *A. leilia.* This error was probably based on Hollands' relabelling of Edwards' collection. In addition, Holland mistakenly considered the type locality of *A. montis* to be Colorado and figured specimens from the Denver area as being typical. "William H. Edwards, when he rearranged his collection before transmitting the same to me, restricted the specific name *montis* to a long series of specimens most of them bred from larvae obtained in Colorado." (Holland, 1931). These specimens are in fact assignable to either *A. celtis antonia* or *A. celtis celtis*, thus further complicating the identity of *A. antonia.*

Holland (1931) also stated, "Edwards . . labeled in his own handwriting as *antonia*, a specimen which bears the label 'Colorado, Dodge, type of *antonia*,' and which agrees thoroughly with other specimens labelled as *antonia* from Texas and Arizona." This specimen was the one mentioned in the original description of *A. antonia* variety *montis* (Edwards, 1883) and which in fact is labelled, "*Antonia* [male]/Colo. Dodge; type of *v. montana.*" Apparently Holland did not resolve the identities of these butterflies according to accepted taxonomic rules and procedures, preferring to rely on Edwards' relabelled specimens. Barnes and McDunnough (1913) were the first to unravel this taxonomic confusion. The problem was finally settled by Brown in 1967 by lectotype designations.

Populations at the edges of the range of this species are the most extreme phenotypically. One such population, called here "mexicana," occurs in southern Texas into northeastern Mexico where it is sympatric with *A. clyton louisa.* It has not yet been possible to define this population geographically in Texas and it seems to blend (clinally) into central Texan *A. celtis antonia.*

Parasites reported to attack *A. celtis* include the hymenopterous parasites *Telenomus* sp. (Scelionidae) of eggs and *Elachertus* sp. (Eulophidae) of last instar larvae, and the fly, *Euphorocera* prob. *floridensis* Townsend (Tachinidae), in larvae of *A. celtis celtis* (Friedlander, 1984). A few eggs of *A. celtis antonia* were found to be parasitized with trichogrammatids in central Texas.

The predator *Polistes exclamans* Viereck (Hymenoptera, Vespidae) of fifth instar larvae attacks individuals of *A. celtis antonia* (Friedlander, 1984).

Asterocampa leilia (W. H. Edwards, 1874)

(Genitalia, Figure 5)

Synonymy and discussion of types

Apatura leilia W. H. Edwards, 1874; F. M. Brown, 1967 (designation of lectotype)
Apatura leila, H. Skinner, 1891 (misspelling)
Apatura celtis? variety *leilia*, H. Strecker, 1878
Apatura cocles, W. H. Edwards, 1884 (manuscript name); J. A. Lintner, (1885) (original description)
Apatura celtis, E. M. Aaron and S. F. Aaron, (1885) (part))
Apatura alicia variety *leilia*, J. B. Smith, (1884)
Apatura alicia, J. B. Smith, (1884) (misidentification)
Doxocopa leilia, F.D. Godman and O. Salvin, (1884)
Doxocopa celtis, F. D. Godman, (1901) (part)
Chlorippe leilia, W. J. Holland, 1898
Chlorippe cocles, H. G. Dyar, [1903]
Chlorippe celtis variety *antonia*, H. Skinner, 1911 (part)
Chlorippe celtis variety *leilia*, H. Skinner, 1911
Asterocampa leilia, J. Röber, 1916; W. J. Holland, 1931; J. McDunnough, 1938; H. Stichel, 1938; C. C. Hoffmann, 1940; A. B. Klots, 1951; J. A. Comstock, 1953 (biology); K. Maeki and C. L. Remington, 1960 (karyotype); C. F. dos Passos, 1964; L. D. Miller and H. K. Clench, 1968 (biology); J. A. Scott, 1973 (biology), 1975 (biology); W. H. Howe, 1975; G. T. Austin, 1977 (biology); R. M. Pyle, 1981; L. D. Miller and F. M. Brown, 1983
Asterocampa leila, J. A. Comstock, 1961; P. R. Ehrlich and A. H. Ehrlich, 1961; L. D. Miller and F. M. Brown, 1981 (misspellings)
Asterocampa leilia form *cocles*, H. Stichel, 1938; D. B. Stallings and J. R. Turner, 1947; A. B. Klots, 1951
Asterocampa leilia cocles, C. F. dos Passos, 1964; L. D. Miller and F. M. Brown, 1983
Asterocampa leila cocles, L. D. Miller and F. M. Brown, 1981 (misspelling)
Asterocampa cocles, J. McDunnough, 1938; C. F. dos Passos, 1964
Asterocampa celtis race *antonia*, J. S. Garth, 1944 (misidentification)
Asterocampa montis, R. M. Pyle, 1981 (misidentification, part: p. [284])
Celtiphaga leilia, W. Barnes and F. H. Benjamin, 1926
Celtiphaga cocles, W. Barnes and F. H. Benjamin, 1926

This species was originally described from 2 males taken in August 1874 by a member of the Wheeler Expedition "at Camp Lowell and in Sonoto [sic] Valley, Arizona" (Mead, 1876). Brown (1967) selected a lectotype which together with the paratype is deposited in the Carnegie Museum of Natural History. Both have been examined.

Lintner's *Apatura cocles* was described from 2 females which he collected in the spring of 1877 in Hidalgo, Texas. He published the manuscript (written in 1880) in 1885 after it had been circulated in the East. These female specimens from Texas in the spring exhibited a phenotype quite different for the species than the type specimens of *A. leilia*. The latter are males from Arizona collected in the late summer. Even so, *A. cocles* was recognized as being the same as *A. leilia* shortly after it was described (Aaron and Aaron, 1884 (1885). Edwards was unfamiliar with the specimens at the time he saw Lintner's manuscript and included *A. cocles* as a Lintner manuscript name in his list (1884a) although he had probably seen females of *A. leilia* by that time from Arizona (from Doll: Edwards, 1883).

One of the 2 syntypes is in the New York State Museum, Albany and the other in the Carnegie Museum of Natural History. The latter syntype is here designated as the lectotype. It is labelled, "Apatura, cocles. [Female], Lintn., 5861. TYPE," "*Linnert* [sic], *Rio Grande*," "Sm. No. 189, det. Skinner," "collect., Skinner," "Asterocampa, leilia (Edw.) [female], det. W. J. Reinthal," "Exch. A. N. S. P., C. M. Acc. 20359.," "Holotype, Apatura, cocles Lintner," "Insect collection, Carnegie Museum of, Natural History, Pittsburgh, Pa. (CMNH)."

Diagnosis

A. leilia belongs to the Celtis group of Skinner (1911). This species is unique in that it uses only one species of hackberry, *Celtis pallida* Torr., as a larval host and is not likely to be found on any other. There are chemical and morphological differences between species of this subgenus of hackberry (*Momisia*) and that of the tree species. *A. leilia* overlaps the range of *A. celtis antonia* in Texas, Mexico and Arizona, the only member of the Celtis group with which it is sympatric and is often confused. Only the "mexicana" population of *A. celtis antonia* is known to use *C. pallida* as a larval host plant.

Eggs of *A. leilia* differ from those of other members of the Celtis group by having a thicker chorion and smaller aeropyles.

Larvae of *A. leilia* differ from members of the Celtis group by having more strongly developed dentition and branched head setae in the first instar. The antlers of mature larvae are proportionately longer while other head scoli are shorter. The whole head capsule is thicker and less hairy. The body setae are shorter and cuticle thicker. Dentition is more pronounced in mature larvae as well.

Larvae of *A. leilia* are solid green with dorsolateral and subspiracular yellow longitudinal stripes, whereas *A. celtis antonia* larvae routinely have some lateral yellow crenations or diagonal stripes. *A. leilia* larvae have green faces centrally but are variously brown dorsally and laterally elsewhere on the head. The antlers resemble the spination of the host plant. *A. celtis antonia* larvae have brown antlers and from green to brown heads. Intermediate forms of *A. celtis antonia* have brown streaks from the mandibles up the the antlers, on a green background.

A. leilia pupae are unique among hackberry butterflies by having a reduced cremaster, the hooks spanning only half the distance from the posterior tip to the sustainers. As a consequence, the pupae hang away from their substrate (usually a twig instead of a leaf) instead of being flush against it. The effect is that of being very leaf-like instead of being hidden by a leaf. Pupae are surprisingly hairy, with the setae being bent at right angles as possibly an adaptation for moisture retention. There is very little in the way of light markings on carinae such as are found on pupae of *A. celtis antonia* except for those on the wing edges and the dorsal crest.

Adult butterflies have the wing shape of members of the Clyton group but the color pattern of the Celtis group. As Edwards (1874) stated, "[*Leilia* is] allied to *Celtis*, but with the shape of *Clyton*." Both discal bars are unbroken, most eye-spots are well developed, and the FW postmedian spots are distinctly white. Other Celtis group taxa have a broken discal bar, often have a few eye-spots reduced, and the FW postmedian spots tend to be yellowish.

Descriptions of life stages

The mature larva and pupa were described by J.A. Comstock (1953). The larva was illustrated on the wrong host plant, *Celtis reticulata*, instead of *Celtis pallida*. The latter is the correct host. The figured pupa was attained through rearing and was slightly misshapen.

EGGS AND EGG DEPOSITION:

Egg with 19 or 20 ribs, 0.9 mm wide, sculpturing obscured by thickened chorion, micropylar area in 3 ranks, 9 petals in rosette, aeropyles very small. Eggs deposited in small clusters (3-15) on either side of leaves of host plant. Egg yellowish white.

LARVAE:

First instar larva with brownish black head capsule and green body, 2.6 mm long. Head capsule 0.6 mm wide, excluding scoli, setae barbed; 5 pairs of scoli prominent, twice width of simple eye. Mandiables 4-toothed. Body setae as long as those on head, also barbed. Prolegs with well developed crampets. Anal area short spinose; anal horns long, light brown.

Second instar larva with well developed antlers and long lateral head scoli, body length 3.9 mm. Head capsule 0.85 mm wide, excluding scoli. Dark brown head, green body, with some indication of dorsolateral longitudinal stripes.

Third instar larva 0.8 mm long, with noticeably short body setae and heavily sclerotized head capsule. Certain sets of body chalazae have fused bases.

Diapausing form with smaller head and shorter, clubbed antlers. Head capsules 1.1-1.3 mm wide. Brown head, green body, with beginnings of subdorsal and supraspiracular, yellow longitudinal stripes.

Fourth instar larval head capsule takes on typical *A. leilia* look with squarish head and long, short-branched antlers, width 1.8-2.2 mm. Coloration as in fifth instar.

Fifth instar larval head capsule 2.5-2.8 mm wide; body with very short setae dorsally. Texas populations generally with longer head scoli than those of Arizona. Mandibles still with teeth, the one incisor with a wavy edge. Antlers 1.7 mm long, AL about as long as antler is wide, longer than AM. AT1 and AB1 short, AB2 long, AB3 short, AB4 very short, AB5 short. V1 and V3 short, V2 vestigial. L1 long, 0.7-0.9 mm. O2 same length as AB2, O3 slightly shorter. Other head scoli short or vestigial as shown. Antlers dark reddish brown to black, concolorous with top and sides of head capsule; face green except for stemmatal region, upper part of median facial sclerite, which are also dark brown. Labrum and sides of face (where green meets brown) light colored (yellowish white). Body olive green, nonreflective, almost grayish green, matching the coloration of host plant leaves, heart-line barely showing. Dorsolateral and subspiracular longitudinal stripes yellowish white, more intense on thorax, running from head capsule to short anal horns. Spiracles whitish to light green. Texan larvae with lighter head capsules, reddish brown less extensive, head often green laterally. Total length about 27 mm.

PUPAE:

Pupa typical of *Asterocampa*, except for shortened cremastral bed of hooks, 1.45 mm. Pupa about 15-18 mm long, 4.5 mm wide, 6.8-8.5 mm high. Head with short prolongations; eyes each with small tubercle. Abdominal crest not abrupt, divisions between segments noticeable but not serrated, anterior segmental portions blunt (not spinose). Crest, head carinae and edges of wings marked with light yellow; rest of body olive green, blending into coloration of leaves. Texas pupae with more light-colored markings especially laterally on abdominal segments in the form of speckles, a subspiracular line, and the beginnings of diagonal stripes. Reduced cremaster holds pupa away from substrate at about 30 degree angle.

ADULTS:

Asterocampa leilia (Pl.21, figs. A-C) antennal scape and pedicel white-scaled; flagellar segments (36-44) scaled dorsally with dark brown ending distally with white scales, bare ventrally between carinae. Club virtually bare, composed of 12 segments, cuticle dark brown dorsally and laterally on first 5, pale yellow orange beyond. Frons black, scaled on dorsal two-thirds with short whitish scales intermixed with long, light grayish brown hair-scales. Palps with short white and long pale yellow scales on basal 2 segments. Basal segment with brush. Second and third segments with brown scaling laterally and medioventrally. Third segment mainly brown, except for white tip and ventral long-scales. Occiput with short white strap- and long light grayish brown hair-scales. Body dorsally orange rufous short-scaled, with grayish brown hair-scales, black cuticle of thorax showing through. Abdomen appearing more orange. Body ventrally mainly white with scattered brown. Forelegs white. Middle and hindlegs dorsally pale yellow orange.

Costal FW length (fig. 4) 20-25 mm (male, 22.1 ± 1.4 mm, n = 54), 23-30 mm

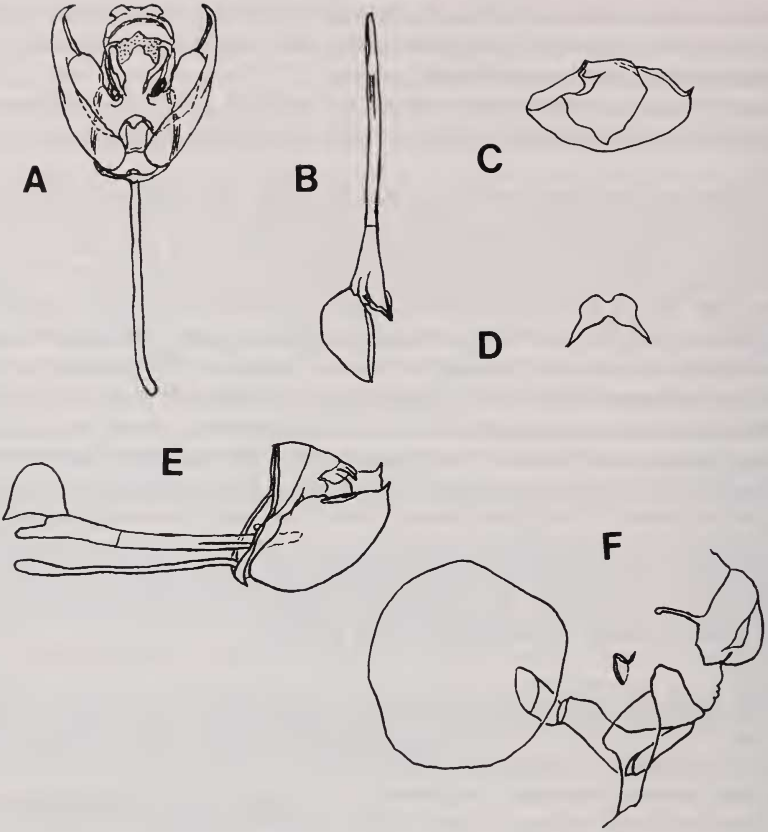

Fig. 5. Genitalia of *Asterocampa leilia* (Edwards).
Male genitalia:
Whole genitalia (**A**, ventral view, valves spread) with aedeagus (**B**) separate: Texas: Dimmit Co., Chaparral Wildlife Management Area, July 1977, A. Lewis, coll. TF gen. prep. 1977.
Right valve (**C**, mesal view) and uncus (**D**, ventral view): Mexico: Veracruz, Jalapa, no date, CMNH. TF gen. prep. no. 1982-9.
Whole genitalia (**E**, left lateral view): Arizona: Pima Co., Soldier Canyon, April 1928, CMNH. TF gen. prep. no. 1982-99.
Female genitalia:
Whole genitalia (**F**, left lateral view): Arizona: Pinal Co., 10 mi. w. Superior, May 1978, CMNH. TF gen. prep. 1982-47.

(female, 26.1±1.6 mm, n = 24); females from Texas generally larger than those of Arizona and central Mexico.

Male genitalia (Fig. 5A-E) with moderate saccus (2.1-2.4 mm) and aedeagus (2.9-3.0 mm). Valves 1.5-1.7 mm long with developed costal ridge and short terminal spine. Uncus reduced, lobes flattened posterolaterally, notch slight. Anal tuft present, hair-scales straight. Female genitalia, (fig. 5F) with short, sclerotized ductus (0.7-1.5 mm) meeting long ostiolar funnel. Corpus bursae with a pair of signa, in longitudinal strips on the right side, sometimes not well sclerotized. Anal papillae not emarginate.

Photographs of adults published in: Brown, 1967 (Fig. 20, lectotype, male, d, v); Ferris and Brown, 1981 (p. 356, male, d); Pyle, 1981 (Plate 662L, male, v; Plate 663L, male, d); Pyle, 1985 (Plate 662L, male, v; Plate 662R, male, d); Scott, 1986 (Plate 19 [figs.] 141a, male, d; 141b, male, v); Wright, 1906 (Plate XXIII: fig. 246, male, d). Howe (1975) excellently figured individual specimens (Plate 11: fig. 13, female, d; fig. 15, male, d; fig. 15, female, v).

Forewings dorsally with basal ground color strong orange (a rich, intense orange) infuscated with grayish brown at base; dark brown distally, changing in reflectance to more reddish when viewed at an angle; costal margin orangish out towards apex. Two discal bars dark brown with reddish brown centers, pale orange-yellow between. Postmedian spots in zigzag pattern (R5-A2), white anteriorly, pale yellow posteriorly; spots bordered basally with dark brown. Limbal spots white in R5 and M2, brownish black with whitish pupils in M1 and M3, brownish black in Cu1. Spots M3 and Cu1 ringed with strong orange. Ocellus Cu2 represented by strong orange spot, sometimes with black center. Veins dark brown, as are submarginal and marginal bands. Fringe dark brown with white centrally in triads in cells R5 to Cu2+A1.

Dorsal HW ground color strong orange, except anal cup and costal cell, which are light gray. Discal cell faintly 2-barred, reddish brown with mixed dark brown scaling. Postmedian spots pale yellow, bordered basally with reddish brown with mixed dark brown, obscure. Limbal spots brownish black in local fields of orange-yellow, with at least spot Cu1 pupilled with bluish white. Veins dark brown. Submarginal band crenated dark brown; marginal band dark brown; fringe checkered as in FW cells Sc+R1 to Cu2+A1. Hair-scales cover lower basal portion of wing to hind angle, pale orange.

Forewings ventrally dark grayish brown above Cu2 and chestnut brown basally in cell Cu2+A1. Discal cell 2-barred, dark brown with lighter middles, white between. Postmedian spots whitish, the more posterior ones tinged with brown, bordered basally with dark brown. Limbal spots as follows: R5 white; M1, M3 Cu1 dark brown with whitish blue pupils in strong yellow ring; M2 dark brown with yellow ring basally, white distally. Submarginal band brown, broken into crescents; marginal band dark brown, appearing almost purplish, in field of grayish scaling such as dusts anterior margin of FW and basal half of HW. Veins brown.

Hindwings ventrally largely cast in grayish scaling except margins of spots and other features of wings. Bars of discal cell dark brown in outline; similar spot basally in cells Sc+R1 and Rs. Postmedian spots whitish, bordered basally with dark brown. Limbal spots dark brown with whitish blue pupils in strong yellow rings bordered by dark brown, Sc+R1 to A2; Cu2 and A1 spots joined at yellow ring.

Variation observed among individuals included larger whitish blue pupils on limbal spots, decreased size of limbal and postmedian spots, darker scaling between discal bars dorsally, broader fields of orange surrounding limbal HW spots dorsally (females), dorsal ground color almost yellow-orange (spring season specimens, especially from Arizona)

Range

A. leilia (Plate 2): Southern Texas and Arizona, northern Mexico: Gila River drainage in southern one-half of Arizona, south into Sonora and Baja; Rio Grande drainage, except Pecos River, northward to Llano Basin in Texas; in northeastern Mexico, rivers in the Chihuahuan desert, and river drainages from Nuevo Leon to Veracruz. Specimens examined (states listed alphabetically, by county; over 850 non-reared adults):

MEXICO: Chihuahua, Coahuila, Durango, Nuevo Leon, Sonora, Tamaulipas, Veracruz [states]

U.S.A.: ARIZONA: Cochise, Gila, Maricopa, Pima, Pinal, Santa Cruz, Yavapai; NEW MEXICO: Hidalgo; TEXAS: Bexar, Brewster, Cameron, Frio, Hidalgo, Jeff Davis, Kerr, Live Oak, Maverick, Presidio, Starr, Terrell, Uvalde, Val Verde, Webb, Zapata; UTAH: Weber [extremely dubious record].

The distribution of this butterfly is coincident with that of its host plant, *Celtis pallida* Torrey. It occurs at lower altitudes, in arroyos, canyons, chaparral and thorn forest. The Weber Co., Utah record is outside the known distribution of its host (Benson and Darrow, 1945) and must be considered either a misidentification or a mislabeling. The Washington Co., Utah record of Callaghan and Tidwell (1971(1973)) is probably *A. celtis antonia* ["montis"] (Gillette, pers. comm.). The specimens reported as *A. leilia* from the Grand Canyon (Garth, 1950) are actually *A. celtis antonia* ("montis") (Reinthal, unpublished obs.). *A. leilia* has recently been documented to occur in Baja California del Sur, Mexico (Brown and Faulkner, 1984).

Discussion

Asterocampa leilia is unique among hackberry butterflies in that it utilizes only spiny hackberries (*Celtis* subgenus *Momisia*) as larval food plants. Larvae and adults (Austin, 1977; pers. obs.) are active at high temperatures. Males prefer perches on the ground. Adults are commonly sap-feeders but are also found at flowers, scat and rotting fruit. They are often found in association with *A. celtis antonia.*

Adults of *A. leilia* are often and easily confused with *A. celtis antonia. A. leilia* was discovered at the same time as the western populations of *A. celtis* were being described and because it was not very different in pattern or hue was often included as another western form of *A. celtis.*

The distinctness of this species is best seen by its host plant utilization and in its larvae and pupae which are adapted to the host plant and high temperatures. Larvae and pupae are virtually impossible to locate on *Celtis pallida* because they are cryptically colored and of a similar size to the leaves. Larval antlers resemble developing paired spines of the plant. Pupae hang at an angle resembling a leaf.

Egg parasites (hymenoptera: Scelionidae, *Telenomus* sp.) have been reported for this species (Friedlander, 1984).

Asterocampa clyton (J. B. A. Boisduval and J. E. Le Conte, [1835])

(Genitalia, Figure 6)

Synonymies and discussion of types

Asterocampa clyton clyton (J. B. A. Boisduval and J. E. Le Conte, [1835])

Apatura clyton J. B. A. Boisduval and J. E. Le Conte, [1835] (biology); W. H. Edwards, 1877 (biology), 1881 (biology), 1884 (biology), 1884 (evolution); M. E. Murtfeldt, (1886) (biology); H. Edwards, 1889 (biology); L. O. Howard, 1894 (ecology)
Apatura elyton, W. A. Pearce, 1894 (misspelling)
Apatura proserpina S. H. Scudder, (1868); F. M. Brown, 1983 (citation)
Apatura idyja, W. F. Kirby, 1871 (part)
Apatura idyja, W. V. Andrews, 1875 (misspelling, part)
Apatura herse, C. V. Riley, 1873 (biology), 1874 (biology)
Apatura hyrse, H. G. Knaggs *et al.*, (1874) (misspelling)
Apatura clyton variety *proserpina*, W. H. Edwards, (1876) (biology); C. J. Maynard, 1891
Apatura clyton dimorphic variety *proserpina*, W. H. Edwards, 1877, 1884; W. Osburn, 1895 (excluded name)
Apatura clyton aberration *proserpina*, H. Strecker, 1878
Apatura clyton variety *ocellata* W. H. Edwards, (1876); J. B. Smith, 1903
Apatura proserpina S. H. Scudder, (1868)
Apatura proserpina ocellata, W. G. Wright, 1905
Apatura clyton aberration male *nig*. H. Strecker, 1878 (abbreviated name, excluded name)
Apatura clyton nig J. B. Smith, 1903 (misspelling, change in status)
Doxocopa herse, S. H. Scudder, 1871 (1872)
Doxocopa clyton, F. D. Godman and O. Salvin, (1884)
Chlorippe herse form *clyton*, S. H. Scudder, 1875
Chlorippe herse, S. H. Scudder, 1881
Chlorippe clyton, S. H. Scudder, 1888 (biology, morphology), 1889 (biology); W. J. Holland, 1898 (biology); J. W. Tutt, (1906) (biology); R. A. Leussler, 1913 (evolution); V. Randolph, 1929 (evoluation); A. H. Clark, 1932 (biology)
Chlorippus clyton, W. T. Davis, 1924 (misspelling)
Chlorippe herse variety *proserpina*, S. H. Scudder, 1875, 1889; H. Engel, 1908; R. A. Leussler, 1913 (evolution); F. E. Watson, 1920 (evolution)
Chlorippe clyton variety *nig*, H. Skinner, 1911
Asterocampa lycaon, J. Röber, 1916 (part)
Asterocampa lycaon aberration *ocellata*, J. Röber, 1916 (excluded name)
Asterocampa clyton, W. J. Holland, 1931 (biology); J. McDunnough, 1938; H. Stichel, 1938; R. W. Macy and H. H. Shepard, 1941 (biology); G. Ehle, 1950 (biology); A. B. Klots, 1951; C. F. dos Passos, 1964; R. Heitzman, 1965 (biology); P. R. Ehrlich and A. H. Ehrlich, 1961 (part); W. H. Howe, 1975; J. A. Scott, (1981) (biology); R. M. Pyle, 1981) L. D. Miller and F. M. Brown, 1981, 1983; P. A. Opler and G. O. Krizek, 1984 (biology)
Asterocampa clyton aberration *nig*, J. McDunnough, 1938 (excluded name)
Asterocampa clyton from *nigra*, H. Stichel, 1938

Asterocampa clyton form *proserpina*, J. McDunnough, 1938; H. Stichel, 1938
Asterocampa clyton form *ocellata*, H. Stichel, 1938
Asterocampa clyton form "apunctus" J. A. Scott, 1981 (excluded name)
Celtiphaga clyton, W. Barnes and F. H. Benjamin, 1926
Celtiphaga clyton aberration *nig*, W. Barnes and F. H. Benjamin, 1926 (excluded name)
Celtiphaga clyton form *proserpina*, W. Barnes and F. H. Benjamin, 1926

Like *A. celtis, A clyton* is based on a drawing by John Abbot of Georgia. Any specimens used for the drawing are presumed destroyed so that the figure itself must be considered as the type. The lectotype (Brown, 1967) of *A. clyton* var. *ocellata* Edwards (female, Coalburgh, West Virginia) is in the Carnegie Museum of Natural History and has been examined. The type of Scudder's *A. proserpina* (female, Iowa) has not yet been located. It was not found at the Museum of Comparative Zoology at Harvard University where it was last reported to be deposited (Miller and Brown, 1981). Both names have been long known to represent color forms. The male type (Berks Co., Pa.) of *Apatura clyton nig* J. B. Smith, 1903, is in the Strecker Collection presently housed at the Allyn Museum of Entomology in Sarasota, Florida. Poorly marked "apunctus"-like individuals (Scott, 1981) occur in virtually all populations of *A. clyton*.

Asterocampa clyton flora (W. H. Edwards, 1976)

Apatura clyton variety *flora* W. H. Edwards, (1876); H. Edwards, 1889 (biology)
Apatura flora, W. H. Edwards, 1881 (biology), 1882 (biology), 1884 (biology), (1891) (biology)
Chlorippe flora, W. J. Holland, 1898
Chlorippe clyton variety *flora*, H. Skinner, 1911
Asterocampa lycaon form *flora*, J. Röber, 1916
Asterocampa flora, W. J. Holland, 1931; W. H. Howe, 1975; L. D. Miller and F. M. Brown, 1981, 1983; R. M. Pyle, 1981
Asterocampa clyton, P. R. Ehrlich and A. H. Ehrlich, 1961 (part)
Asterocampa clyton flora, J. McDunnough, 1938; H. Stichel, 1938; L. Harris, Jr., 1950 (biology); A. B. Klots, 1951; W. M. Davidson, 1958 (biology); C. F. dos Passos, 1964; P. A. Opler and G. O. Krizek, 1984
Celtiphaga clyton flora, W. Barnes and F. H. Benjamin, 1926

This taxon is based originally on several males and a female collected in Palatka, Florida. Brown (1967) designated (with Reinthal) one of the males as lectotype which together with the remaining type series is housed in the Carnegie Museum of Natural History. These have been examined.

Asterocampa clyton texana (H. Skinner, 1911)

Apatura flora, E. M. Aaron and S. F. Aaron, (1885); F. H. Snow, (1906) (misidentifications)

Chlorippe clyton variety *texana* H. Skinner, 1911; W. Barnes and J. McDunnough, 1913
Chlorippe flora, J. K. Strecker, 1925 (misidentification)
Chlorippe clyton subpallida W. Barnes and J. H. McDunnough, 1913 (new synonym)
Asterocampa lycaon, J. Röber, 1916 (part)
Asterocampa texana, W. J. Holland, 1931; J. A. Comstock, 1961 (biology); W. J. Reinthal, 1966 (biology); W. H. Howe, 1975; L. D. Miller and F. M. Brown, 1981, 1983; R. M. Pyle, 1981
Asterocampa subpallida, W. J. Holland, 1931; J. A. Comstock, 1953 (biology); C. F. dos Passos, 1964; W. H. Howe, 1975; L. D. Miller and F. M. Brown, 1981, 1983; R. M. Pyle, 1981
Asterocampa clyton texana, J. McDunnough, 1938; H. Stichel, 1938; A. B. Klots, 1951; C. F. dos Passos, 1964; R. W. Neck, 1977 (biology); C. J. Durden, 1982 (evolution)
Asterocampa clyton subpallida, J. McDunnough, 1938; H. Stichel, 1938; W. D. Field, 1940 (partial misidentification); J. A. Scott, (1981) (biology)
Asterocampa leilia, J. A. Comstock, 1953 (misidentification, part: pp. 130-132)
Asterocampa clyton, P. R. Ehrlich and A. H. Ehrlich, 1961 (part)

The male holotype, female allotype and other specimens of the type series of *Chlorippe clyton* from *texana* (Round Mountain, Texas) are in the Carnegie Museum of Natural History. Syntypes (2 males, 4 females) of *Chlorippe clyton subpallida* (Baboquivera [sic] Mts., Pima Co., Arizona) are in the National Museum of Natural History, Smithsonian Institution. The male lectotype is designated here ("Babaquivera [sic], Mts. Ariz., Pima Co." "C. clyton, v. subpallida, Type [male] B & McD" "Photograph, Pl. 2 No. 7" "Aug") and is housed in the museum type collection.

Asterocampa clyton louisa (D. B. Stallings and J. R. Turner, 1947)

Asterocampa clyton louisa D. B. Stallings and J. R. Turner, 1947; A. B. Klots, 1951; C. F. dos Passos, 1964
Asterocampa louisa, W. H. Howe, 1975; L. D. Miller and F. M. Brown, 1981, 1983; R. M. Pyle, 1981

The holotype male of *Asterocampa clyton louisa* (Pharr, Texas) is in the Yale Peabody Museum. It has not yet been examined.

Diagnoses of taxa

Asterocampa clyton belongs in the Clyton group of hackberry butterflies. The nominate subspecies differs from *A. clyton texana* and the similar *A. clyton lousia* in both larval and adult stages. The caterpillars are routinely fully striped whereas those of *A. clyton texana* and *A. clyton louisa* generally lack subdorsal and lateral banding, being marked only with crenations and lines. Adults are tawny, contrastingly marked with dark brown, and exhibit dark morphs in which the hindwing limbal spots are partially ("ocellata") or fully obscured ("proserpina"). Spot Cu1 of the FW is not ringed. Cu1 ringed is the condition commonly seen in *A. clyton texana* and *A. clyton louisa*.

A. clyton flora differs only slightly from the nominate subspecies. Larvae routinely have shorter antlers than their more northern and western counterparts; adults are considerably larger and more colorful, the browns of the wing apices being replaced by a brick red orange; dark forms "proserpina" and "ocellata" are virtually absent in both sexes. It differs from *A. clyton texana* and *A. clyton louisa* by the same characters as does *A. clyton clyton*. *A. clyton flora* occurs in peninsular Florida and forms hybrid zones with typical *A. clyton clyton* on both the Gulf and Atlantic coasts. There is a tendency of both large size and bright coloration in populations of *A. clyton clyton* along the Gulf Coast producing an adult phenotype similar to *A. clyton flora*.

The larvae of *A. clyton texana* and *A. clyton louisa* have longer antlers than found in the other subspecies and the body color is mostly green (with lines and crenations of yellowish white) rather than being typically striped. Larvae of *A. clyton texana* generally have heads which are mostly green whereas those of *A. clyton louisa* are typically mostly dark brown. Adults of both subspecies are far less orange than the adults of the eastern subspecies and tend to have lighter ground colors of tan. The apices of the forewings of *A. clyton louisa* are very dark. Limbal spot Cu1 of the FW is often ringed with darker scaling. Limbal spots of the HW below are often "washed out," especially in *A. clyton texana* form "subpallida." Dark forms in either sex have not been reported but a few such individuals occur in both wild and laboratory populations. *A. clyton texana* and *A. clyton louisa* will be discussed together in the following descriptions

Descriptions of life stages

Immature stages of *A. clyton clyton* were described in detail by Riley (1874), Edwards (1876, 1884d), and Scudder (1889). Immature stages of *A. clyton flora* were described by Edwards in 1881 and 1891. Stamp (1983) reported on the diapause behavior of third instar larvae. Immature stages of *A. clyton texana*, forms "subpallida" (first instar, second instar, mature larva and pupa) and "texana" (all immature stages), were described by J.A. Comstock in 1953 and 1961, respectively. Scott (1986; Pl.2 [fig.] 142; Pl.4 [fig.] 142) photographically illustrated the mature larvae and pupa of *A. clyton clyton*.

EGGS AND EGG DEPOSITION:

Egg of *A. clyton clyton* 19-22 ribbed, 0.7-0.9 mm wide by 0.7-0.9 mm high. Micropylar rosette with 11 petals. Sculpturing smooth, cross-ribbing and aeropyles only apparent on upper half of eggs. Eggs of *A. clyton flora* light yellow, also in large masses, tightly packed in many layers, usually deposited on the undersides of leaves of the larval host plant *Celtis laevigata* Willd. Edwards

(1881, 1891) reported eggs of *A. clyton flora* yellow-green, with 16-20 vertical ribs and 3-4 concentric rows of polygonal areoles in micropylar rosette.

Eggs of *A. clyton texana* and *A. clyton louisa* with thick sculpturing, usually with 20 ribs (18-21), micropylar rosette with 8-12 petals, more western populations (*A. clyton texana* form "subpallida") tending to have fewer petals. Aeropyles only on upper halves of longitudinal ribs. Eggs 0.7-1.0 mm wide, 0.9-1.0 mm high, deposited in moderately large, tightly packed clusters.

LARVAE:

First instar larval head capsule of *A. clyton clyton* tan to dark brown, usually light brown, 0.6 mm wide, with poorly developed head scoli about size of simple eye. Setae of head capsule and body extremely short-branched. Total body length 3.7 mm. Prolegs with crampets; setae unbranched. Body color light green. Anal horns very short. First instar larval head capsule of *A. clyton flora* tan; body light and dark green striped. Total length about 4 mm. First instar larval head capsule of *A. clyton texana* and *A. clyton louisa* light to medium brown, 0.6 mm wide, poorly developed, head scoli short, about size of stemmatal width. Setae of head capsule extremely short-branched (barbed). Body yellowish green; anal horns short. Total length about 4 mm.

Second instar larva of *A. clyton clyton* with patterned brown and cream-colored brown head capsule. Antler base greater than mandibular width. AB5 about 3/4 length of L1. Scoli V2 present. Body green, striping apparent in this stage, consisting of 3 yellow stripes on each side of a darker green heart-line. Anal horns light green. Total length about 4 mm. Second instar larva of *A. clyton flora* with variegated head capsule, half brown. Antlers wider at base than mandibles are wide. AB5 about 3/4 length of L1. V2 present. Body striped as in mature larva. Anal horns unpigmented. Total length between 3 and 4 mm. Second instar larval head capsule of *A. clyton texana* variably marked with brown. Capsule 0.9 mm wide, with conical scoli, antler base wider than mandible, AB5 about 3/4 of L1 in length. Head narrower at level of antlers than at mandibles, not square. Body striped with green and yellowish green. Anal horns unpigmented to light tan. Total length about 6 mm. Second instar larva of *A. clyton louisa* similar to that of *A. clyton texana*, but generally with darker brown head capsule.

Third instar larva of *A. clyton clyton* with mottled brown head capsule. Diapausing larva with reduced antlers. Total length about 7.5 mm. Third instar larva of *A. clyton flora* also with variegated head capsule. Body marked as before. Diapausing larva with reduced antlers. Total length 5 to 6 mm. Third instar larval head capsule of *A. clyton texana* variable, but mostly brown with long scoli (non-diapausing), 1.2-1.5 mm wide. Body striped as in second instar. Total length about 6 mm. Third instar larva of *A. clyton louisa* similar, but yellows more intense, head capsule mostly dark brown.

Fourth instar larva of *A. clyton clyton* with variegated brown head capsule. Total length up to about 20 mm. Fourth instar larva of *A. clyton flora* with brown-streaked head capsule, antlers rather short. Green morphs occasionally occur, with only front of antler brown. Body striped as in mature larva; total length over 10 mm. Fourth instar larval head capsule of *A. clyton texana* variably brown, with long scoli, AL and AM of antler rounded and thick. Head capsule width 2.4-2.5 mm wide. *A. clyton louisa* with darker head capsules with longer antlers. Total length about 13 mm; pigmented as in mature larva.

Fifth instar larva of *A. clyton clyton* green with (usually) green head capsule which has 4 vertical, white stripes (unpigmented areas); antlers have brown dot anteriorly. Heart-line dark green. Subdorsal bands yellow and white, the inner one light yellow with intermittent yellowish white folds, separated from outer by intermittent green. Dorsolateral portion yellowish white. Subdorsolateral area green with lighter center; yellowish white chalazae punctuate center. Supraspiracular band yellowish white. Spiracular area green with yellowish green center; chalazae apparent. Subspiracular stripe yellowish white. Prolegs, venter, and thoracic legs light to medium green. Anal horns long. Some individuals with considerably less yellow to banding. Total length 32-42 mm. Fifth instar larva of *A. clyton flora* green with yellow stripes, with dark brown and green head capsule striped with white; antlers rather short. Heart-line dark green. Subdorsal bands bright yellow, the inner portion more yellow than the outer, which is whitish and separated by a green line. Supra-and subspiracular bands yellow. Length of males, 30-38 mm, females, 35-44 mm.

Fifth instar larval head capsule of *A. clyton texana* with 1.4 mm long antlers, terminal pair of scoli rounded, broad. Head capsule around 3 mm wide. AT1, AB4 short, AB1 and AB3 slightly longer, AB2 longer still, with AB5 very long. V3, V1 and O3 moderately long, O2 longer (about same size as AB5), L1 longest of all (1.1 mm). AB5 to L1 ratio 0.80. Mandible with single incisor. Larvae light green with variably colored head capsules. Capsules are more often green with 4 whitish vertical streaks and a brown spots anteriorly on the antler in the more arid areas of the range (e.g., "subpallida"). *A. clyton louisa* larvae with dark brown head capsules. Heart-line a darker green line than general body color, sometimes invaded by spots of light yellow from the inner portion of the subdorsal bands. Subdorsal bands represented most often only by yellowish white dorsolateral line. Dorsolateral line sometimes intermittent, line alternating with spots of light yellow found in inner subdorsal area, such as normally found in *A. clyton louisa* mature larvae. Supraspiracular area marked with diagonal yellowish white dashes or whitish crenated line. Subspiracular line yellowish white. Anal horns moderately long. *A. clyton louisa* larvae generally much more colorful than those of *A. clyton texana*, with much more yellow and contrastingly colored head capsules, such as found in *A. idyja argus*. Total length about 32-36 mm.

PUPAE:

Pupa of *A. clyton clyton* 18-28 mm long, 7-11 mm high, head prolongations moderately long, somewhat blunt. Body color green, the dorsal crest marked with yellowish white, as are the posterior borders of the wings. Abdominal crest long, finely serrate, each segment with anterior tooth subtended by pair of small black spots. Pupae with cremastral pad lengths of 2.4-3.4 mm. Pupa of *A. clyton flora* 18-26 mm long, about 7-8 mm wide, and 10-12 mm high at maximum height. Head prolongations moderately long, somewhat blunt. Body yellowish green speckled with tiny whitish dots. Dorsal crest marked with whitish, as are veins and posterior edges of wings. Both supra- and subspiracular markings present. Abdominal crest finely serrate, each segment produced anteriorly into a spine subtended by pair of small black spots. Cremastral lengths of pupa 2.8-3.2 mm. Pupa of *A. clyton texana* 17-22 mm long, about 8 mm wide and up to 10 mm high at abdominal segment 3. Head prolongations moderate, blunt. Body light green flecked with white and with whitish markings along dorsal crest (more yellowish posteriorly) and posterior margins of wings. Wing veins and supraspiracular regions (in diagonal bars) also marked with white. Abdominal crest somewhat serrate, anterior ends of segments ending in spines subtended by pairs of small black spots. Pupal cremastral lengths 2.5-3.0 mm. Pupa of *A. clyton louisa* similar to that of *A. clyton texana.*

For a much more complete description of adults of this species the reader should consult my dissertation. Adults of the 4 subspecies differ mainly in coloration rather than pattern or morphology. Major differences among the adults are given in the descriptions to follow.

ADULTS:

Asterocampa clyton clyton (Pl.21, figs. D-I) antennae medium to dark brown, minutely ringed with lighter brown on flagellar segments giving faintly dotted appearance; apical portions slightly swollen, dark brown with bare pale yellow (tan with aging of preserved specimens) tips. Palps, general body scaling and ground color of wings above, strong yellowish orange, infuscated with dark brown. Forewing costal length (Fig. 4) *A. clyton clyton* 21-27 mm (males, 24.6 ± 1.4m, n = 72), 26-34 mm (females, 30.6 ± 1.7 mm, n = 34). Male genitalia (Fig. 6A-E) saccus 3.8-4.8 mm, aedeagus 4.3-5.7 mm, valves 2.2-2.6 mm, uncus bifid with narrow notch, dorsal brush with straight hair-scales. Female genitalia (Fig. 6F): ductus 2.8-3.1 mm, signum usually absent, when present 2 longitudinal strips.

Adults of *A. clyton clyton* illustrated by photographs: Brown, 1967 (female, lectotype of "ocellata," d, v); Ebner, 1970 (p. 96, male, d, v); Ferris and Brown, 1981 (p. 357, male, d, v; female, d); Harris, 1972 (Plate 6: fig. 5, male, d; fig. 6, female, d); Holland, 1898, 1931 (Plate XXIII: fig. 5, male, d; fig. 6, female, d); Lewis, 1973 (p. 13: fig. 7, male, d; fig. 8, female, v); Pyle, 1981, 1985 (Plate 666L, male, v; Plate 666R, female, d); Scott, 1986 (Plate 19 [fig.] 142d, male, d); Watson and Whalley, 1975 (pl. 216p, male, d). Howe (1975) illustrated individual specimens (Plate 11: fig. 10, male, v; fig. 16, male, d; fig. 17, female, d).

A. clyton clyton limbal spots yellow-orange, large, somewhat indented distally by submarginal band. In light phase, ground color basally strong yellowish orange, distally dark brown; hindwing above lighter. In dark phase, varying degrees of infuscation with blackish scaling, obscuring spots, especially in the hindwings.

Asterocampa clyton flora (Pl.21, figs. J-L) antennae of medium brown; apical portions as in nominate subspecies. Palps, general body scaling and ground color of wings above, strong orange. Forewing costal length (Fig. 4) of *A. clyton flora* 23.0-29.0 mm (males, 26.8 ± 2.1 mm, n = 12), 30.5-37.0 mm (females, 33.8 ± 2.4 mm, n = 9). Male genitalia of *A. clyton flora* similar to *A. clyton clyton*: saccus 3.6 mm, aedeagus 5.2 mm, valves 3.7 mm, uncus narrowly notched, dorsal brush with straight hair-scales. Female genitalia: ductus 2.2-2.8 mm long, signum composed of a pair of longitudinally wrinkled areas.

Adults of *Asterocampa clyton flora* illustrated by photographs in: Brown, 1967 (Fig. 22, male, lectotype, d, v); Harris, 1972 (Plate 6: fig. 7, male, d; fig. 8, female, d); Holland, 1898, 1931 (Plate XXIII: fig. 1, male, d; fig. 2, female, d); Pyle, 1981, 1985 (Plate 665, male, v, d);. Excellent figures in Howe (1975: Plate 11: fig. 8, male, v; fig.18, male, d; fig. 19, female, d).

A. clyton flora limbal spots yellow-orange, adjacent to dark brown submarginal band. Ground color basally strong (yellowish) orange, distally dark

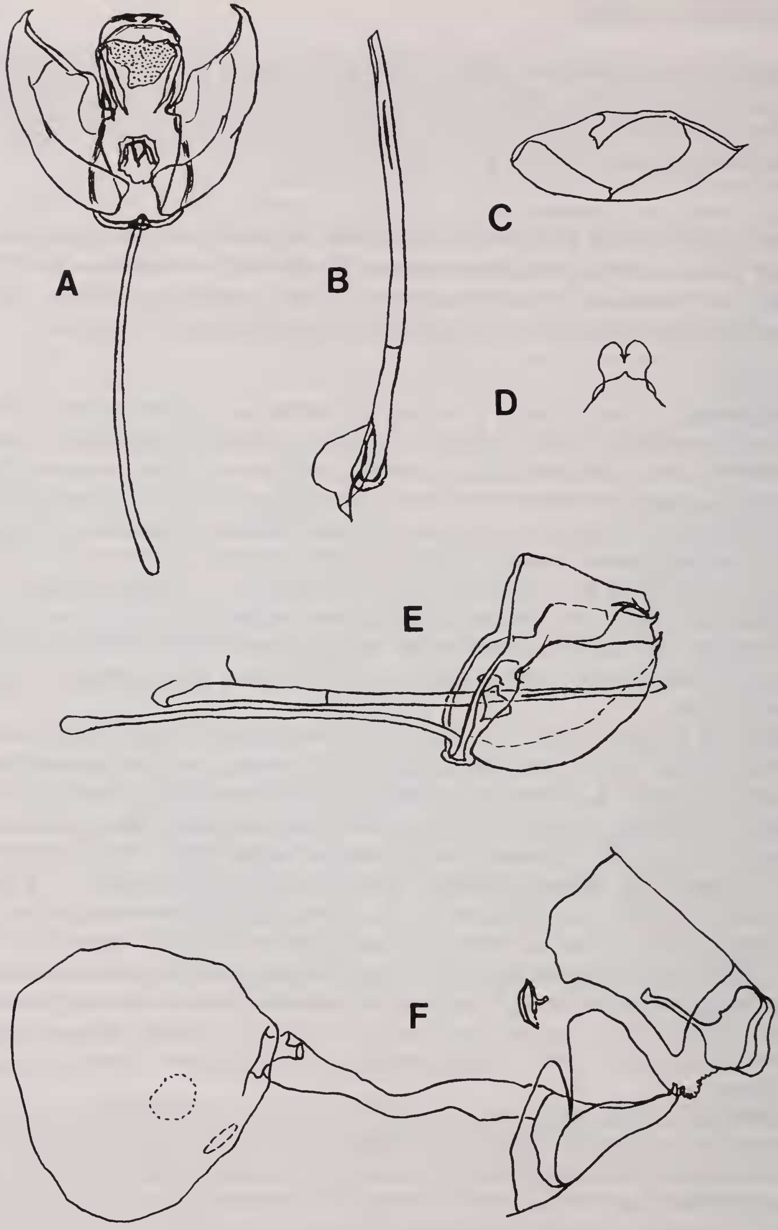

Fig. 6. Genitalia of *Asterocampa clyton* (B. & L.).
Male genitalia:
Whole genitalia (**A**, ventral view, valves spread) with aedeagus (**B**) separate: Texas: Travis Co., Austin, September 1977, T. Friedlander. TF gen. prep. no. 1977. *A. clyton texana* (Skinner).
Right valve (**C**, mesal view) and uncus (**D**, ventral view): Nebraska: Douglas Co., Omaha, June 1913, CMNH. TF gen. prep. no. 1982-28. *A. clyton clyton*.
Whole genitalia (**E**, left lateral view): Texas: Travis Co., Austin, September 1977, T. Friedlander. TF gen. prep. no. 1977. *A. clyton texana*.
Female genitalia:
Whole genitalia (**F**, left lateral view): Texas: Travis Co., Austin, September 1977, T. Friedlander. TF gen. prep. no. 1977. *A. clyton texana*.

brown (males) or brownish orange (tawny; females). Hindwing above paler, yellow-orange.

Asterocampa clyton texana (Pl.21, figs. M-O; Pl.22, figs. A-C) antennae of medium to dark brown, finely ringed with lighter brown on flagellar segments giving faintly dotted appearance when coloration constrasting; apical portions as before. Palps, general body scaling and ground color of wings above, light brownish orange. *Asterocampa clyton louisa* (Pl.19, fig. O; Pl.22, figs. D-F) antennae of very dark brown, only tips cream-colored. Palps, general body scaling and ground color of wings above, brownish orange, infuscated with dark brown. Forewing costal lengths (Fig. 4) of *A. clyton texana*: 23.0-29.0 mm (males, "subpallida", 26.4 ± 1.8 mm, n = 50), 28.0-37.0 mm (famales, "subpallida", 32.3 ± 1.8 mm, n = 29); 20.0-28.0 mm (males, "texana", 24.3 ± 1.5 mm, n = 118), 27.0-37.0 mm (females, "texana", 31 ± 2.3 mm, n = 95); overall, 20.0-29.0 mm (males, n = 168), 24.5-37.0 mm (females, n = 124). Forewing lengths of *A. clyton louisa*: 22.0-26.0 mm (males, 24.8 ± 1.2 mm, n = 17), 24.5-34.0 mm (females, 30.3 ± 2.7 mm n = 9). Male genitalia of both subspecies as for *A. clyton clyton*: saccus 3.1-4.0 mm, aedeagus 4.1-6.9 mm, valves 2.1-2.3 mm, uncus narrowly notched, hair-scales of dorsal brush straight. Female genitalia of both subspecies: ductus 2.6-4.8 mm; usually without signum, but when present, 2 oval patches of polygonal reticulation on right side.

Photographs of adults of *A. clyton texana* in: Barnes and McDunnough, 1913 (Plate II: Fig. 7, "subpallida", male, syntype, d; Fig. 8, "subpallida", female, syntype, d; Fig. 9, "subpallida", female, syntype, v; Fig. 10, "texana', female, v); Holland, 1931 (Plate LX: fig. 6, near "texana", female, d); Pyle, 1981, 1985 (Plate 666L, "texana"?, male, v); Scott, 1986 (Plate 19 [figs.] 142a, male, d; 142b, "subpallida", female, d; 142c, female, v); Stanek, 1977 (fig. 81 [top left], "texana"?, male, d). Photographs of *A. clyton louisa* in: Montgomery, 1984 (pp. 3-4, male, d); Pyle, 1981, 1985 (Plate 661, females, v, d). Howe (1975) ably illustrated individual specimens (Plate 12: fig. 7, near "texana", male, d, v; fig. 8, near "texana", female, d, v; fig. 9, *louisa*, male, d, v; fig. 10, *louisa*, female, d, v; Plate 13: fig. 8, "subpallida", male, d, v; fig. 9, "subpallida", female, d, v).

A. clyton texana and *A. clyton louisa* limbal spots white, Cu1 with brown ring often expressed. Ground color basally light brownish orange, distally chestnut brown (light yellow-orange posteriorly distally). Browns of *A. clyton louisa* much darker, but otherwise similar to *A. clyton texana*. Females tawnier than males.

Range

A. clyton clyton (Plate 3). Eastern United States and extreme southern Ontario, Canada. Specimens examined (states listed alphabetically and by county; over 850 non-reared adults):

CANADA: Ontario (prov.)

U.S.A.: ALABAMA: Marengo, Tuscaloosa; ARKANSAS: Desha, Madison, Pulaski, Washington; CONNECTICUT: Fairfield, Tolland; FLORIDA: Liberty; GEORGIA: Bibb, Chattahoochee, Richmond; ILLINOIS: Adams, Cook, Macon, Madison; INDIANA: Kosciusko; IOWA: Polk, Woodbury; KANSAS: Douglas, Franklin, Greenwood, Johnson, Labette, Riley; KENTUCKY: Edmonson, Garrard, Jefferson, Nelson; LOUISIANA: Jefferson, Orleans, Rapides (parishes); MARYLAND: Allegany, Baltimore, Washington; MASSA-

CHUSETTS: Hampden, Hampshire; MICHIGAN: Genesee, Lenawee, Washtenaw; MISSISSIPPI: Chickasaw, Clay, Hancock, Hinds, Holmes, Lauderdale, Lee, Lowndes, Madison, Oktibbeha, Rankin, Warren, Washington, Wilkinson; MISSOURI: Cass, Clay, Jackson, St. Louis; NEBRASKA: Cass, Douglas; NEW JERSEY: Cape May, Essex, Hudson, Hunterdon, Middlesex, Morris, Sussex; NEW YORK: Dutchess, Kings (Long Island), Orange, Queens (Long Island), Richmond (Staten Island), Tompkins, Westchester; NORTH CAROLINA: Durham; OHIO: Champaign, Franklin, Hamilton, Montgomery; OKLAHOMA: Garfield; PENNSYLVANIA; Allegheny, Beaver, Lancaster, Washington; SOUTH CAROLINA: Charleston, Edgefield, Richland; TENNESSEE: Cocke, Davidson, Hamilton, Knox, Lake, Maury; TEXAS: Angelina, Aransas, Bailey, Baylor, Bowie, Burnet, Coryell, Dallas, Harris, Hill, Houston, Limestone, Live Oak, San Patricio, Tarrant, Travis; VIRGINIA: Dinwiddie, Fairfax, Montgomery, Rockbridge, Wythe; WASHINGTON, D. C.; WEST VIRGINIA: Hampshire, Kanawha.

A. clyton flora: Peninsular Florida, coastal Georgia, rarely into south Carolina. Specimens examined (over 250 non-reared adults):

U.S.A.: FLORIDA: Alachua, Broward, Dade, Hendry, Indian River, Levy, Monroe, Nassau, Orange, Palm Beach, Pinellas, Polk, Putnam, St. Johns, Seminole, Volusia; GEORGIA: Chatham, Glynn; SOUTH CAROLINA: Charleston.

A. clyton texana: Northern Mexico, southwestern United States: southern Arizona, western Kansas, western Oklahoma, western Texas. Specimens examined (over 1,150 non-reared adults) [form "subpallida" (°) (over 350 non-reared adults)]:

MEXICO: Chihuahua, Coahuila, Hidalgo,°? Sonora° [states]

U.S.A.: ARIZONA°: Cochise, Pima, Santa Cruz; KANSAS: Barber, Washington; NEW MEXICO: Eddy; OKLAHOMA: Blaine, Childress, Cleveland, Cotton, Garfield, Kiowa, McClain, Woodward; TEXAS: Armstrong, Atascosa, Bailey, Bastrop, Baylor, Bee, Bell, Bexar, Blanco, Bosque, Brewster°, Brooks, Burnet, Comal, Coryell, Dallas, Dimmitt, Goliad, Gonzales, Hays, Jeff Davis°, Kaufman, Kendall, Kerr, Kleberg, Live Oak, Llano, Maverick, McLennan, Medina, Menard, Nueces, Palo Pinto, San Patricio, Tarrant, Terrell, Travis, Uvalde, Val Verde, Victoria, Webb, Wichita, Williamson counties; also Brazos, Cameron (coastal), Harris rarely.

A. clyton louisa: Far south Texas in lower Rio Grande Valley; northeastern Mexico. Specimens examined (over 350 non-reared adults):

MEXICO; Nuevo Leon, Tamaulipas [states]

U.S.A.: TEXAS: Cameron, Hidalgo, Starr counties.

A female specimen labelled, "Texas: Beeville, Bee Co., June-10-1970, W.H. Howe," in the AMNH is *A. clyton louisa*. Perhaps this is a stray or a phenocopy, rather than a mislabelling. A reared male specimen labelled, "Bastrop, 18.VI.62," in the AMNH is probably from Brownsville.

Discussion

A. clyton is not a particularly common butterfly unless its habits are known to the observer. Adult butterflies stay near the host plant. The egg masses and gregarious larvae are easily found by parasitoids and predators according to Riley (1873). Such an oviposition strategy as depositing eggs in large masses would presumably have been selected for the increased survival of offspring (genetically similar larvae). Larvae have evolved predator avoidance and defensive behaviors.

Several incorrect host records have been reported for this species and for *A. clyton clyton* in particular. For a discussion of these records the reader should consult my dissertation.

A. clyton flora is related to *A. clyton clyton* just as *A. celtis reinthali* is related to *A. celtis celtis*. These taxa of the Florida peninsula have evidently been isolated from the more mainland populations of their respective species. Individuals are larger in size and could be given as examples of "island gigantism" within the genus. Was it during the Pleistocene that populations of these butterflies were isolated in limestone sinks with their host plants? The central peninsula of Florida has been thought to be a refugium during the Pleistocene for a few butterflies (Klots, 1965).

A. clyton louisa is fairly distinct and has only limited zones of intergradation with the similar *A. clyton texana*. These zones are found on the northern edges of its range, coastally north of Brownsville, and inland, up the Rio Grande above Starr County, Texas. The larvae have dark heads in contrast to their colorful bodies. Adults are progressively darker southward into Mexico. The form "subpallida" of *A. clyton texana* occurs in the western end of the distribution of the typical form "texana" and is synonymized. On the whole, western populations are lighter in color and have less distinct markings. More field work is needed to determine if either *A. clyton louisa* in eastern Mexico or *A. clyton texana* ("subpallida") in western Mexico (northern Sonora where it presumably occurs) overlaps the range of *A. idyja argus*.

The hymenopterous parasites *Telenomus* sp. and *Tetrastichus* sp. attack eggs of *A. clyton clyton* (Friedlander, 1984). Both tombstone pupae (Clausen, 1940) (Hymenoptera: Eulophidae, *Elachertus* sp.) and the attached banded barrel-shaped cocoons of the ichneumonid wasp *Microcharops tibialis* (Cresson) are frequently found in association with middle instar larvae. Both *Cotesia* and *Meteorus* species (Hymenoptera: Braconidae) have been reared from *A. clyton clyton* larvae. Larvae are presumably attacked by tachinid flies, as other species are. Larvae are also subject to predation by bugs, ants and vespid wasps. The larval parasites *Meteorus* sp. and *Cotesia* sp. have been reared from middle instar larvae of *A. clyton flora* by N. Stamp (det. Friedlander). The whole range of insect parasites and predators that have been recorded for hackbberry butterflies has been reported for members of *A. clyton texana* or *A. clyton louisa* (Friedlander, 1984).

Asterocampa idyja **(Geyer, [1828])**

(Genitalia, Figure 7)

Synonymies and discussion of types

Asterocampa idyja idyja **(Geyer, [1828])**

?*Papilio herse* J. C. Fabricius, 1793 (identity obscure; junior homonym of *Papilio herse* Hufnagel, 1766)
Doxocopa idyja C. Geyer, [1828]; J. Gundlach, 1881 (biology)
Nymphalis idyja, D. F. Poey, 1847
Apatura idyja, (E. Doubleday), *et al.*, (1850)
Apatura idyia, W. H. Edwards, (1873) (misspelling)
Apatura clyton, W. F. Kirby, 1871 (part)
Apatura herse, H. Strecker, 1878
Chlorippe idyja, W. F. Kirby, 1901
Doxocopa idyja padola H. Fruhstorfer, 1912
Asterocampa lycaon from *idyja*, J. Röber, 1916; D. M. Bates, 1935
Asterocampa clyton idyja, H. Stichel, 1938
Asterocampa clyton padola, H. Stichel, 1938
Asterocampa argus idyja, W. P. Comstock, 1944
Asterocampa idyia, N. D. Riley, 1975 (misspelling)
Asterocampa idyia form *padola*, N. D. Riley, 1975 (misspelling)
Asterocampa lydia, E. Welling, 1981 (misspelling!)

The type of *Doxocopa idyja* is presumed to be lost. It is represented by figures 3 and 4 of plate [13] in (Hübner, J. and) C. Geyer, 1826-1841 [1828], *Sammlung exotischer Schmetterlinge*, 3 (Hemming, 1937). Figure 3 is of an adult female in dorsal view with well defined post-median spots in the FW and ocellate limbal spots in the HW. Figure 4 is a ventral view of a well marked adult female. There is no surviving manuscript description accompanying the plate. The illustrations are to be considered as representing the type.

The holotype of *Doxocopa idyja padola* is in the Staudinger collection housed in the ZMHU in Berlin and has been examined. The description is based on the male which exhibits a greater degree of orange scaling than does the illustration of *D. idyja*. It is from an unspecified location in Haiti ("Haiti, 25/10 96. Hopke" "*Doxocampa* [sic], *idyja padola*, Fruhstorfer" "Typus" "Zool. Mus., Belin"). A specimen of *A. idyja idyja* has recently been collected on the northern coast of Haiti (Nord: Cormier Plage) (Schwartz, 1983) and others have been taken near Cap-Haitien. Specimens from many other localities on Hispaniola (in the Dominican Republic) fill out the known range of color variation of this subspecies.

Asterocampa idyja argus **(H. W. Bates, 1864)**

Apatura argus H. W. Bates, 1864
Doxocopa argus, F. D. Godman and O. Salvin, (1884)
Apatura ([=]Doxocopa) argus, O. Staudinger (and E. Schatz), (1888)
Doxocopa argus form *armilla* H. Fruhstorfer, 1912 (excluded name)

Asterocampa argus, J. Röber, 1916; C. C. Hoffmann, 1940
Asterocampa argus from *armilla*, J. Röber, 1916 (excluded name)
Doxocopa idyja var. *argus*, A. Hall, 1916 [1983] (microfiche)

The type specimen of *Apatura argus* (Bates) is in the BM(NH) (Godman and Salvin, 1884; Gabriel, 1927; Stichel, 1938). This holotype is a male from the Motagua Valley [El Progresso; Lamas, pers. comm.] in Guatemala ("Motagua, valley" "Apatura, argus, Bates" "[male]" "Type, H. T." "Type., Sp. figured." "Motagua, Valley., F. D. G. & O. S." "B. M. TYPE, No. Ph. 9126., Apatura, argus, [male] Bates." "B. C. A. Lep. Rhop., Doxocopa, argus, Bates., Godman-Salvin, Coll. 1916-4.").

Doxocopa argus form *armilla*, based on 2 females (Hannemann, pers. corr.), is a color form and not representative of a geographically or genetically isolated population. Fruhstorfer (1912) and Röber (1916) indicated that specimens of both sexes exhibited the band. It is the typical and more common form of *A. idyja argus* found throughout the range of this subspecies. The lectotype (designated here) is in the ZMHU, Berlin. It is from Honduras ("Hond., Wittk." "*Doxocampa* [sic], *argus armilla*, Fruhst." "Typus" "Zool. Mus., Berlin"). I have not seen the paralectotype. I have not yet found any reference to "armilla" that uses this excluded form name as a subspecies name (potentially validating the name).

Diagnosis

A. idyja idyja is separated from *A. idyja argus* best by its geographic location in the Greater Antilles. Not enough is known about the immature stages to differentiate these stages from *A. idyja argus*, but preliminary studies of fifth instar larval head capsules and pupal cases indicate near morphologial identity. At least some, and perhaps all, individual larvae of *A. idyja idyja* have less pigmented head capsules than those of *A. idyja argus*. *A idyja idyja* adults resemble the dark forms of both sexes of *A. idyja argus* but are more subdued in color and somewhat smaller in size. I know of no adults of *A. idyja idyja* exhibiting the characteristic post-median band of the FW found in the light form of *A. idyja argus*.

A. idyja argus is most easily differentiated from *A. idyja idyja* by its geographic location in Central America (including Mexico). The adults of *A. idyja argus* are slightly larger and more brightly colored. In addition, most specimens are of the light form, the postmedian spots of the FW expanded and forming a narrow golden (yellow) band across the discal area similar in appearance to the pattern found in a number of other butterflies in Central America and Mexico.

Descriptions of life stages

Gundlach (1881) provided brief descriptions of the mature larva and pupa of *A. idyja idyja*. All of the immature stages of *A. idyja argus*, except the first and second instar larvae, are desribed in Friedlander (1986a).

EGGS AND EGG DEPOSITION:

Egg of *A. idyja idyja* presumably of Clyton group type, deposited in masses. Egg of *A. idyja argus* typical of Clyton group, 19-20 ribs, 0.8 mm wide by 0.9 mm high, deposited in large clusters (300 ± eggs). Micropylar rosette with 66-8 petals.

LARVAE:

Larva of *A. idyja idyja* typical of Clyton group, with variably black head and anal horns, body striped with yellow and green. Lightly pigmented larvae, with mostly green heads and green anal horns, are known.

Mature larva of *A. idyja argus* of Clyton group type, 3-4 cm long, head and body (maximum) 5 mm wide; anal horns short, each 1 mm long. Head capsule black, hairy, with whitish patches on lower face and posteriorly on antlers. Mandibles with a single cutting edge. Body integument studded with white chalazae bearing short colorless setae. Spiracles whitish. Body longitudinally striped with shades of yellow and olive green with black anal horns. Heart-line black. Subdorsolateral band greenish black with olive center; spiracular band olive green with intermittent yellow center; prolegs and venter olive green. Subdorsal, supraspiracular and subspiracular bands light yellow. Olive green line separates inner subdorsal band from outer (dorsolateral) band. Intensity of yellow in bands varies.

Third and fourth instar larvae do not differ in any major way from mature larvae except in size; earlier instar larvae not yet described.

PUPAE:

Pupa of *A. idyja idyja* green, similar to that of *A. idyja argus*.

Pupa of *A. idyja argus* typical of *Asterocampa*, 2.1-2.6 cm long, 0.7-0.9 cm wide, 0.9-1.2 cm high at abdominal crest (third segment). Pupa yellowish green with whitish markings on head and body carinae. Diagonal white stripes on sides of abdominal segments 2-7 between crest and spiracles, higher ends posterior. Head prolongations blunt. Metanotum very short medially (longitudinally). Anterior median edges of third through eighth abdominal segment produced into spines, subtended by pairs of black spots. Length of cremastral bed of hooks 3.5-4.1 mm.

ADULTS:

Antennae of *A. idyja idyja* (Pl.22, figs. G-I) brown above, with white tufting at lateral bases; front tan above, white below; pair of white tufts mesal to chaetosemata; palps brown above, white below, tan mesally; occiput scaling white laterally (seen as 2 lateral dots from above). Body light brown, orange brown above, light tan below; femora 2 and 3 darker dorsally, tibiae and tarsi 2 and 3 tan, as are foretibiae mesally; tan to brown posteriorly, to genitalia. Body above same color as basal ground color of HWs, but black color of cuticle shows inbetween scaling. Vertex and patagia same color as costal cell of FWs. Costal FW length (Fig. 4) of *A. idyja idyja* 24.0-29.0 mm (males, 26.3 ± 1.5 mm, n = 8), 34.0-37.0 mm (females, 35.0 ± 10 mm, n = 7). Male genitalia (Fig. 7E): long aedeagus (5.0-5.5 mm) and saccus (3.8-4.5 mm). Valves 2.2-2.3 mm long; uncus bilobed with deep notch, as in *A. idyja argus*. Terminal tuft composed of straight hair-scales dorsally on intersegmental membrane 8-9. Female genitalia: long,

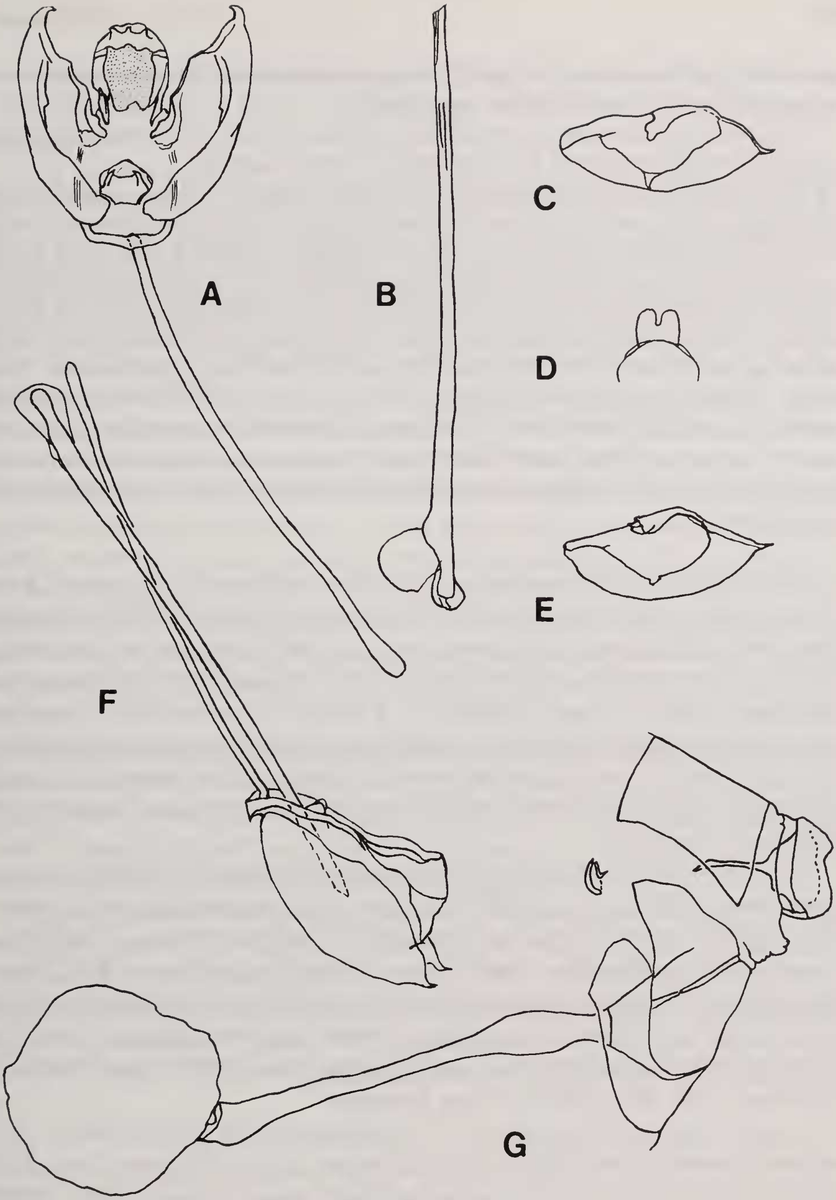

Fig. 7. Genitalia of *Asterocampa idyja* (Geyer).
Male genitalia:
Whole genitalia (**A**, ventral view, valves spread) with aedeagus (**B**) separate: Honduras, no date, CMNH. TF gen. prep. no. 1982-23. *A. idyja argus* (Bates).
Right valve (**C**, mesal view) and uncus (**D**, ventral view):: Mexico: Oaxaca, 2.1 mi. nw. Totolapan, July 1981, reared, T. Friedlander. TF gen. prep. no. 1982-1. *A. idyja argus*.
Right valve (**E**, mesal view): Cuba, no date, CMNH. TF gen. prep. no. 1982-2. *A. idyja idyja*.
Whole genitalia (**F**, left lateral view): Honduras, no date, CMNH. TF gen. prep. no. 1982-23. *A. idyja argus*.
Female genitalia:
Whole genitalia (**G**, left lateral view): Mexico: Veracruz, Jalapa, no date, CMNH. TF gen. prep. no. 1982-48. *A. idyja argus*.

sclerotized ductus (3.8 mm) adjoining large ostiolar funnel. No signum observed on corpus bursae. Anal papillae emarginate.

A. idyja idyja figured in Comstock (1944: Plate 7, Figure 9). Male in dorsal and ventral view illustrated in N. D. Riley (1975: pl. 4, fig. 3).

FWs dorsally with basal ground color tawny (medium brown scales mixed with orange ones, with more orange anteriorly in the discal cell); discal cell with 2 bars, close together, the more basal one obscure, indicated with dark brown scaling, almost separated into 2 separate spots, the more apical one dark brown, at end of discal cell; apical ground color dark brown (medium dark to dark brown scaling), interrupted by lighter marginal and submarginal bands, and 5 white limbal spots (R5 to Cu1); veins brown; pale yellow-orange postmedian spots nearly alligned in slight zigzag (R5 to A1); fringe dark brown with white centrally in cells R3 to Cu2+A1. Variation: amount of brown scaling increased, infuscating base of wing; postmedian spots reduced in size in females; orange scaling in discal areas increased; cell M2 with yellow-orange spots just beyond apical discal bar.

Hws dorsally with ground color tawny, infuscated by brown hair-scales, light grayish brown scales in anal cup; discal markings virtually obscured; limbal spots dark brown, surrounded by orange-yellow scaling (R5 to A1), some with whitish pupils (Cu1); veins brown; submarginal, marginal bands, fringe (Sc+R1 to Cu2−A1) as in FW. Variation observed in orange scaling surrounding eye-spots (increased), infuscation increased, eye-spot size decreased, number of eye-spots with pupils increased; males with more orange surrounding eye-spots, females with rings only (ocellate).

Wings ventrally with patterns of dorsal side repeated in lighter tones; apical area of FW and all of HW washed with tan scaling; veins brown. FW basally, below discal cell, grayish to reddish brown, discal bars concolorous; postmedian spots large, virtually confluent; FW limbal spots white. HW limbal spots dark brown with large whitish blue pupils, surrounded by yellow rings inside orange to brown edging. Variation observed included browns replaced by light orange. HW limbal spots not expressed (R5, M2, M3) in some females.

A. idyja argus (Pl.22, figs. J-O): Antennae dark brown above, each segment dorsally with black scaling terminating in brown; front light brown above, white below; palps medium brown above, white below, light brown mesally, occiput scaling white laterally. White tufting at lateral bases of antennae and mesal to chaetosemata. Body color above brown, black coloration of cuticle showing through, with a few orange scales mixed (same as HW basal ground color); patagia hair scales same as FW costal cell, but strap scales light brown with white mixed. Body ventrally light brown, becoming darker posteriorly. Legs tan. Costal FW lengths (Fig. 4) 28.0-31.0 mm (males, 29.1 ± 1.2 mm, n = 18), 34.0-40.0 mm (females, 36.9 ± 1.8 mm, n = 11). Male genitalia (Fig. 7A-D, F): long saccus (4.3-5.5 mm) and aedeagus (5.5-6.9 mm). Valves 2.2-2.6 mm long; uncus with 2 rounded lobes separated by deep notch. Dorsal tuff of hair-scales on membrane 8-9 straight. Female genitalia (Fig. 7G): long, sclerotized ductus (4.6 mm) joining large ostiolar funnel. Anal papillae emarginate.

Only published figures of *A. idyja argus*, to my knowledge, in *Biologia Centrali Americana* (vol. 38, Godman and Salvin, 1879-1901 (1884), Pl. 30, figs. 12, 13 (male), 14 (female)) and in Seitz (ed.), *Die Großschmetterlinge der Erde* (vol. 5, Röber, 1907-1924 (1916), Pl. 109 (male)).

Dorsal FW with basal ground color bright tawny (orange and brown scaling mixed); discal bars faint, brown, close together; distal ground color dark brown (almost black); veins brown basally, darker apically; limbal spots white (R5 to Cu1); orangish yellow postmedian spots typically enlarged, those in R5 and M1 joined with similarly colored spots beyond apical discal bar, the whole effect being a "golden" band dividing wing (tawny basally and black apically); "dark from", postmedian spots separate as in *A. idyja idyja*, submarginal and marginal bands extremely faint apically, becoming lighter (yellow-orange) at tornus, merging with band in typical from) fringe dark brown with white centrally in cells R3 to A1 (or Cu2+A1). Variation: frequency of dark form, black fades in museum specimens, amount orange scaling.

HW dorsally with ground color tawny infuscated with brown obscured by grayish brown hair-scales basally; anal cup grayish brown; no indication of discal bars or postmedian spots; veins brown; limbal spots dark brown (R5 to Cu2) surrounded by ring (females and dark males) or block (normal males) of orange scaling; submarginal and marginal bands orange typically to grayish or reddish brown (dark form); fringe as in FW, but with wider white rows of scales.

Wings ventrally with same pattern as dorsal side, but lighter. Tan scaling in apex of FW and throughout HW; veins, discal markings and subtending line of postmedian spots in HW brown. Variation: size of ocelli in limbal HW spots, amount of lighter tan scaling, amount dark brown in Cu1 limbal spots FW (ringedness), thickness of postmedian band FW (base of cell M3 good measure), washing out of HW (females, Rs).

Range

A. idyja idyja (Plate 4): Great Antilles — Cuba, Isle of Pines, Hispaniola, Puerto Rico. Localities of specimens examined (over 100 non-reared adults):

CUBA: Granma, Guantanamo, Habana, Isla de Pinos, Pinar del Rio, Santiago de Cuba [provinces]

HISPANIOLA: Haiti (Nord, l'Ouest), Dominican Republic (Altagracia, Barahona, La Romana) [countries (provinces)]; PUERTO RICO: Coamo Springs, San German, Salinas, Quebradillas [cities].

A. idyja argus (Plate 4): Mexico, Guatemala, Honduras, Nicaragua (possibly El Salvador, Belice; not known from Costa Rica, Panama, Colombia, southward). Localities of specimens examined (over 150 non-reared adults):

MEXICO: Chiapas, Guerrero, Hidalgo, Jalisco, Michoacan, Morelos, Nayarit, Oaxaca, Puebla, San Luis Potosi, Sonora, Tamaulipas, Veracruz [states]
HONDURAS: San Pedro Sula [city]
GUATEMALA [no locality given]

One should expect *A. idyja argus* to be found also in Sinaloa, Colima, Mexico, Tlaxcala, and potentially Nuevo Leon and Tabasco in Mexico, where tree-like *Celtis* species grow. Specimens reported (as labelled) from Bogota, Colombia are in reality from Honduras, the faded original labels having been replaced with the erroneous locality label. This butterfly's range is apparently limited by its host plants (and habitat destruction). *Celtis schippii* Trel, ex Standl. needs to be investigated as a possible host of the subspecies in the wetter areas of Central America.

Discussion

The type specimen of *Doxocopa idyja* was part of a collection from Cuba sent to Hübner about a decade earlier than plate [13] was published. The plate was probably drawn before 1823 when figures of other specimens from Cuba were published (such as those of *Lucina* [sic] *sida* and *Siderone nemesis*).

A. idyja idyja is found along river systems coastally where its food plant, *Celtis trinervia*, grows. The butterfly must now be considered to be rare due to habitat destruction over most its range. The immature stages need to be rediscovered and described thoroughly.

The literature record of *Ardisia* as a larval host plant (e.g., Riley, 1975) is probably the result of either misinterpretation or misidentification. In the description of the immature stages of *A. idyja idyja*, Gundlach (1881) stated that he was not entirely sure of his plant identification ("La oruga viva sobre un arbol, *que creo sera* el Agracejo de sabana (Ardisia cubana)," italics added). Möschler (1890) repeated the record without comment that the larva was found on *Ardisia*. W. P. Comstock (1944) cited Gundlach and added that a number of specimens of *A. idyja idyja* had been reared in Hispaniola on a species of *Celtis*. This rearing was mentioned again in Brown and Heineman (1972). A few cast larval and pupal skins are in the AMNH, and the latter are on *C. trinervia* Lam.

A. idyja idyja remains the least well known hackberry butterfly. The sometimes black head and anal horns of the late instar larvae noted by Gundlach (1881) and the short metanotum of the pupa are diagnostic for *A. idyja*. The larval body is striped like some eastern larval populations of *A. clyton* but tends to have more intense shades of yellow and green (olive). N. D. Riley's (1975) abbreviated description of the mature larva, preseumably based on Gundlach's article, is in error in stating that the larvae have orange (instead of yellow, "amarilla" in Gundlach) longitudinal body stripes.

A. idyja argus has been recorded from *Celtis caudata* Planch. (Friedlander, 1986a) in southern Mexico. *C. reticulata* Torr. is used as the host plant in northwestern Mexico and *C. laevigata* Willd. is used in northeastern Mexico. *C. trinervia* should be the host in Central America These trees grow along streams and rivers and on limestone outcrops in seasonally dry lowlands. Species in the *Momisia*-group of hackberries are not considered suitable hosts. Possible reasons for their unsuitability include chemical differences between these and other plants in the genus, microhabitat differences in temperature in which the plants are found, and differences in the size and architecture of the plants. Unless *Celtis schippii* proves to be unsuitable as well, there is no obvious reason for *A. idyja argus* not to be found farther south than it has been. Lamas (pers. comm.) confirms that the butterfly has not been found in South America.

One of the more interesting features of *A. idyja argus* is its light form ("die Armspange" as Fruhstorfer (1912) put it). Many other nymphaloid butterflies within the range of this subspecies share this wing pattern. Notable among these are species of *Smyrna* (especially females), *Historis, Hypanartia* and the brassolid genus *Opsiphanes*. The high percentage of light individuals in the southern part of the range of *A. idyja argus* may well be due to selection for the mimetic resemblance. It is not known if populations occurring in Sonora or Tamaulipas have dark form females. Dark females, apparently more common in Central America, resemble the crepuscular *Pycina zelys*, a tropical nymphalid. The latter color form also occurs in *A. idyja idyja*.

How did this species become distributed across the Greater Antilles, Mexico and Central America? Was a barrier crossed to attain the island/mainland distribution or did the butterfly's range once span the two (by land bridge or pre-drift) and then become disjunct? In which area did the butterfly originate? The phenotypic appearance of *A. idyja idyja* shows the strongest resemblance to that of *A. idyja argus* from Central America. What evidence there is to support one hypothesis over another will be presented in the next section.

Scelionid parasites of eggs (*Telenomus* sp.) have been reported (Friedlander, 1984) from a clutch found in Oaxaca.

PHYLOGENY AND BIOGEOGRAPHY OF HACKBERRY BUTTERFLIES

The hackberry butterflies have been recognized as constituting a natural group for 100 years (Godman and Salvin, 1884; Barnes and McDunnough, 1912). They were given their valid name *Asterocampa* by Röber in 1916. No published revisions of the genus have appeared since the last date.

Hackberry butterflies are in the Apaturinae (Stichel, 1938). This subfamily of butterflies is poorly defined (Niculescu, 1965) but its members do share a number of traits, some of which might be interpreted as synapomorphies. DeVries *et al.* (1985) place the apaturines near the base of the nymphaloid phylogenetic tree on the basis of mostly larval characters analyzed cladistically.

The application of cladistic methodology to butterfly classification has been successful, especially as applied to higher taxa (nymphaloids, DeVries *et al.*, 1985; higher taxa of Papilionidae, Hancock, 1983; genera of Parnassiinae, Hiura, 1980; families, Kristensen, 1976). Phylogenetic revisions of butterfly genera have also been published (Ackery and Vane-Wright, 1984; Hiura, 1981; Jong, 1978; Smiles, 1982). An early review of cladistic classification as applied to Lepidoptera is given by Nielsen (1979).

PHYLOGENY:

Adult apaturine butterflies, as well as several satyrid, nymphaline and charaxine butterflies, were studied for shared derived characters (synapomorphies). References on the morphology and biology of the other life stages of these butterflies were searched, in cases in which specimens were not available for study. Detailed morphological work was carried out on all life stages of the hackberry butterflies and character states compared with those found in other apaturines (outgroup comparisons). Characters found to be useful in the construction of a hypothesized phylogeny of hackberry butterflies are discussed in this revision.

Two-state characters investigated for the life stages of hackberry butterflies selected to constuct the cladogram in this section are listed in Table 9. Each is discussed with regard to the distribution and polarity of its character states. The polarities of characters are largely hypothesized by out-group comparison, as shown in the table.

The sister group to the Apaturinae, which is certainly among the nymphaloid butterflies, is not yet recognized. Many different nymphaloids were examined in an effort to hypothesize synapomorphies which might define the subfamily can be viewed as symplesiomorphies (indistinct antennal club, open discal cells, larvae without body scoli), or if they are apomorphic, the character states recur within the Nymphaloidea, and the characters are not necessarily synapomorphies. Several characters (host plants, larval head morphology, adult genitalia and wing pattern) were found to have merit in defining the Apaturinae.

GENITALIA: Le Moult (1950) and Niculescu (1965) recognized that the long aedeagus and saccus of male genitalia serve to define the Apaturinae. I agree with their views.

HOST PLANTS: A wide variety of angiosperms are used as larval hosts for nymphaloid butterflies (Ackery, 1984). Apaturines use only a small number of plant genera confined to (possibly) four plant families: Betulaceae (*Ostrya*), Fagaceae (*Quercus*), Salicaceae (*Populus, Salix*) and Ulmaceae (subf. Ulmoideae: *Trema, Ulmus, Zelkova*; subf. Celtidoideae: *Celtis, Gironniera*).

Graeser (1888) reported that *Mimathyma schrenckii* (Menetries) pupae were on *Ostrya* and the *Mimathyma nycteis* (Menetries) larvae lived on *Ulmus*. No further reports confirm these findings. *Sephisa dichroa* (Kollar) has been cited as using *Quercus incana* Roxb. (Fagaceae) as its larval host (Mackinnon and de Niceville, 1897; Moore, 1899). That their host is an oak seems unlikely, and even Moore's illustrations of larvae and pupae show them associated with a *Celtis*-looking host. Recently, Görgner (1984) published the host plant of *Euapatura mirza* Ebert as *Zelkova crenata* Spach, but his photographs indicate (as judged by the pinnipalmately veined leaves) that the host is a species of *Celtis* (or possibly that *Z. crenata* is misclassified?).

The Salicaceae (Salicales) are unique among the Dilleniidae in many characters, but are thought by most authors to be closest to the Violales. Fossils belonging to *Salix* have been found dating to the Eocene of North America (Cronquist, 1981). Both *Salix and Populus* are widespread, but they are not found in the Indoaustralian biogeographic realm. Only one genus of Apaturinae, *Apatura*, is known to use Salicaceae as larval hosts.

Other nymphaloid taxa using Salicaceae include some Limenitini and Nymphalini. Some Argynnini and a few Charaxinae feed on members of the Violales (Ackery, 1984; Smart, 1977).

Chemical studies by Giannasi (1978) and palynological data (Zavada and Crepet, 1981) on ulmaceous genera support Grudzinskaya's (1967) conclusions that the celtidoids form a distinct group from the ulmoids. Cronquist (1981) cites Grudzinskaya's feeling that perhaps the Celtidoideae are closer to the Moraceae than the Ulmaceae. The Ulmaceae belongs with the Barbeyaceae, Cannabaceae, Moraceae, Cecropiaceae and Urticaceae in the Urticales (Hamamelidae) (Cronquist, 1981).

Other nymphaloid taxa having Celtidoideae as larval hosts include the Libytheinae and *Polygonia*-like Nymphalini. Other nymphalines (e.g., Coloburini, Marpesiini), Calinaginae, and some danaines feed on Cannabaceae, Cecropiaceae, Moraceae, or Urticaceae (Ackery, 1984; pers. obs.).

It is my feeling that the sister group of the Apaturinae will be found among those butterflies using Urticales as larval hosts. The apaturine butterflies appear to have specialized early on only the Celtidoideae of the Ulmaceae, while other nymphalines which might be considered as possible sister groups and which use Ulmaceae as larval hosts feed on the Ulmoideae genera as well. Within the Apaturinae I think the Celtidoideae are the primitive host plants (Celtidoideae as larval hosts would be a synapomorphy for the Apaturinae). With this view the use of Salicaceae is an advance, perhaps a synapomorphy for *Apatura*, just as *Quercus* would be for *Sephisa*.

LARVAL HEAD MORPHOLOGY: Many nymphalöid caterpillars have antlers at the vertices of the head capsule (e.g., Müller, 1886; also, DeVries *et al.*, 1985). Apaturine caterpillars have antlers which are bifurcate at the tips. Each antler has a small number of subordinate scoli in definite patterns. Apparent specializations in other nymphaloid groups having antlers include terminal antler clubs or spikes, the latter often accompanied by a subtending rosette of scoli. Antlers found among the Marpesiini are highly elongate and curved. The primitive pattern for apaturines and their closest relatives would apear to be like that shown by the antlers of *Calinaga*, which are moderately long, straight, blunt and warty, with each wart supporting a seta. Various warts could then be modified into subordinate scoli. The basic pattern for Apaturinae is, I believe, shown by the antlers of *Sasakia* (see: Shirozu and Hara, 1979).

WING PATTERN: There is an apparent dominance of limbal spot Cu1 in the forewing of apaturine butterflies. The basic nymphaloid wing pattern of concentric rows of spots and bands described by Schwanwitsch (1924) and Süffert (1929) and modified by Nijhout (1978, 1980a) and others, is used here as a starting point for evaluating such evolutionary modifications. One modification of this primitive design found in apaturine (and just a few other nymphalid butterflies, e.g., *Baeotus, Cyrestis, Kallima*) is the retention of limbal spot Cu1 (various losses in expression of the other limbal spots), especially in the forewing.

This pattern might represent a synapomorphy for the Apaturinae, or alternatively, a symplesiomorphy, if those other nymphalines share the trait inherited from a common ancestor.

One notion strikes me when thinking about the Apaturinae. There seems to be a natural division between those genera which exhibit blue iridescence and those which do not. Blue iridescence might well be a symplesiomorphy in the Apaturinae.

Within the Apaturinae there are a few discernable clades. Of immediate interest in this revision are the hierarchical clades containing *Asterocampa*. Three characters, pattern of scoli on larval head antlers, form of pupal cremaster, and male genitalia, are useful in discussing these hypothesized clades.

The number and position of basal subordinate scoli on the antlers among apaturine larvae is variable. There appears to be a basic pattern of a few scoli in vertical rows on the antler below the terminal pair (forked tip of antler). In various lines within the Apaturinae different sets of subordinate scoli are emphasized or suppressed. In the line leading to *Asterocampa* many scoli are suppressed, leaving only five basal scoli and the terminal pair subtended posteriorly by a single scolus. This pattern is apparently shared only by *Chitoria, Dilipa* and *Euapatura*, and possibly, *Thaleropis*, but because the larvae are not known to the author for a few of the other apaturine genera, there is reason to suspect some of the other genera as sharing this condition as well.

A smaller clade within the first might be defined by *Chitoria* and *Asterocampa*, which appear to share a pupal synapomorphy. These are the only 2 apaturine genera known to have a greatly elongated cremastral pad (Edwards, 1878b; Muroya *et al.*, 1967; Riley, 1880). The cremastral hooks extend in a "Y"-shaped pad anteriorly to the level of the sustainers.

Looking at *Asterocampa* for possible synapomorphies turned up only one morphological character which might serve to define the genus. A survey of the morphology of the uncus of apaturine male genitalia revealed that only *Asterocampa* has a broad, bilobed uncus, whereas all the other genera investigated, including *Chitoria*, have an elongate, narrowed and pointed uncus.

One of the more striking features of *Asterocampa* as compared with other apaturine genera is its retention (or re-expression) of fully developed eye-spots, particularly on the undersides of the hindwings. This feature is perhaps best viewed as a symplesiomorphy. It could also represent the derepression of expression of these spots, in which case, the character might be viewed as synapomorphic.

The geographic distribution of apaturine genera may be used with caution as a multi-state character or as an independent set of biogeographic characters with which to test area relationships against morphological relationships. Considering the former, *Asterocampa* is the only extant Nearctic apaturine genus. The shale fossil apaturine (?!) butterfly from the Late Oligocene of Florissant, Colorado, *Chlorippe wilmattae* Cockerell (1907), occurs with fossil *Celtis* (Lamotte, 1952), establishing the presence of such butterflies in North America at a time consistent with one hypothesis for the arrival of the ancestors of hackberry butterflies. Members of the Neotropical genus *Doxocopa* are invading North America at the present time, and probably had done so prior to the Pleistocene. The geographic position of hackberry butterflies is considered by me to be apomorphic relative to *Chitoria* and all the other apaturine genera which are Old World in distribution (I think *Doxocopa* is a South American, Southern Hemisphere, endemic genus). Colonization of North America from eastern Asia could well have been the first step in the evolution of *Asterocampa*.

Next, the characters listed in Table 9 will be discussed. These characters are the basis of the hypothesized relationships among hackberry butterflies. Characters are first examined by the technique of Wagner Network analysis and a Wagner Tree is produced by rooting this network of taxa. Cladistic methodology is then applied by hypothesizing synapomorphies among the polarized characters, and the resulting cladogram compared to the Wagner Tree. Apparent homoplasious characters and synapomorphies are discussed in relation to sister group pairs in the cladogram. Finally, a phylogeny of the hackberry butterflies is hypothesized based on this character set.

1. The chorion between the longitudinal ribs of the eggs is smooth to quite wrinkled in hackberry butterflies. There is no apparent reason to conclude that wrinkling is the derived condition other than the observation that eggs of other Apaturinae (admittedly, these have not been extensively studied) are not known to have this condition. *Euapatura mirza* Ebert (Görgner, 1984) eggs might have this condition. Only the Celtis group of *Asterocampa* exhibits wrinkling.

2. Aeropyles normally occur along the entire length of the exposed

Table 9. Distribution of character states among hackberry butterfly taxa relative to other Apaturinae.

Characters	**States**	**LEI**	**ANT**	**CEL**	**REI**	**TEX**	**LOU**	**CLY**	**FLO**	**ARG**	**IDY**	**OUT-GR**
EGG:												
1. sculpturing	smooth chorion between ribs	–	–	–	–	×	×	×	×	×	×	most
	wrinkled chorion between ribs	×	×	×	×	–	–	–	–	–	–	some?
2. aeropyles	whole length of ribs	×	×	×	×	–	–	–	–	–	–	all?
	lacking basally on ribs	–	–	–	–	×	×	×	×	×	×	none?
3. clutch size	small (1-50), rarely structured	×	×	×	×	–	–	–	–	–	–	most
	large (50-500), structured	–	–	–	–	×	×	×	×	×	×	few
4. host plant	Nearctic *Celtis*	–	×	×	×	×	×	×	×	×	×	other
	Celtis pallida (Neotropical)	×	×	–	–	–	–	–	–	–	–	*Celtis,etc.*
LARVA:												
5. head horns	AB5 of antler>(1/2)L1	–	–	–	–	×	×	×	×	×	×	most
	AB5 of antler≤(1/2)L1	×	×	×	×	–	–	–	–	–	–	some
6. body pigmentation	lines and crenations only	×	×	×	×	×	–	–	–	–	–	most
	additional longitudinal bands	–	–	–	–	–	×	×	×	×	×	some
7. feeding behavior	not gregarious as early instars	×	×	×	×	–	–	–	–	–	–	all?
	gregarious as early instars	–	–	–	–	×	×	×	×	×	×	none?
PUPA:												
8. thorax	metanotum>abdomen 1	×	×	×	×	×	×	×	×	–	–	most
	metanotum<abdomen 1	–	–	–	–	–	–	–	–	×	×	some
9. abdominal keel	anteriorly sharp	–	–	–	–	×	×	×	×	×	×	some
	anteriorly blunt	×	×	×	×	–	–	–	–	–	–	most
10. cremaster	elongated to sustainers	–	×	×	×	×	×	×	×	×	×	*Chit.*
	not reaching sustainers	×	–	–	–	–	–	–	–	–	–	most
ADULT (Wings):												
11. discal bars	basal bar solid	×	–	–	–	×	×	×	×	×	×	most
	basal bar forming 2 spots	–	×	×	×	–	–	–	–	–	–	some
12. postmedian spots	M2 beyond M3	×	×	×	×	×	×	×	×	–	–	some
	M2 and M3 adjacent	–	–	–	–	–	–	–	–	×	×	many
13. limbal spots (FW)	M1, M3 and Cu1 eyespots	×	×	–	–	–	–	–	–	–	–	few
[multi-state]	M3 partially expressed	–	–	×	×	×	×	×	×	×	×	few
14.	M1 partially expressed	–	–	–	–	×	×	×	×	×	×	few
15.	Cu1 without pupil	–	–	×	×	×	×	×	×	×	×	some
16.	A2 present	×	–	×	×	–	–	–	–	–	–	none
	A2 absent	–	×	–	–	×	×	×	×	×	×	all
ADULT (Terminalia):												
17. anal brush (males)	straight	×	×	–	–	×	×	–	×	×	×	some
	recurved	–	–	×	×	–	–	×	–	–	–	none
18. uncus (m)	broadly notched	×	×	×	×	–	–	–	–	–	–	none
	narrowly notched	–	–	–	–	×	×	×	×	×	×	few
19. valve/saccus (m)	v/s>0.7	×	×	×	×	–	–	–	–	–	–	some
	v/s≤0.7	–	–	–	–	×	×	–	×	×	×	most
20. valve/aedeagus (m)	v/a>0.65	–	×	×	×	–	–	–	–	–	–	some
	v/a<0.45	–	–	–	–	–	–	–	–	×	×	many
GEOGRAPHIC RANGE:	western N. America	×	×	–	–	×	×	–	–	×	–	
	estern N. America	–	–	×	×	–	–	×	×	–	–	
	peninsular florida	–	–	×	×	–	–	–	×	–	–	
	Central America	–	–	–	–	–	–	–	–	×	–	
	Greater Antilles	–	–	–	–	–	–	–	–	–	×	

longitudinal ribs of the eggs. The position of the aeropyles corresponds with the ends of the ladder-like horizontal costulae found between the ribs. Aeropyles are absent on the lower halves of the ribs only in the Clyton group of *Asterocampa*.

3. The number of eggs in a clutch ranges from 1 (deposited singly) to well over 500 in a mass for hackberry butterflies. Not many butterflies, and few apaturines, deposit their eggs in distinct clusters consisting of hundreds of eggs. The most space-saving packing design for spherical units such as these eggs approximate is tetrahedral. The behavior necessary for stacking eggs in such a uniform design is more complex than that necessary to place eggs more randomly, whether in piles or

singly. Even though members of some populations of the Celtis group of *Asterocampa* are known to deposit fairly large clutches, the eggs are not strictly tetrahedrally packed as they are in masses deposited by females in the Clyton group. There are few reports of egg depositing behavior in other Apaturinae.

A character correlated with large clutch size is oviposition on mature (old) leaves. This character sate is tentatively considered a derived character state. From the viewpoint of leaf toughness new leaves are both thinner and less tough than old leaves, providing more suitable food for early instar larvae. Chemistry (toxins, deterrents) and nutrition obviously enter into the determination of host suitability. New leaves were found to sustain maximal growth of all hackberry butterfly species in early instars so that there would appear to be no outstanding palatability problem in *Celtis* other than toughness. Early instar larvae of the Clyton group feed gregariously on old leaves and so appear to have made this great food resource available, whereas single larvae are apparently unable to sustain growth on old leaves (personal observations on larvae of both *A. clyton* and *A. celtis*). However, there could be a complicating factor to the interpretation that individual larvae are unable to sustain growth on old leaves if behavioral problems arise due to isolation of a gregarious feeder from external cues from its normal feeding partners (Kalin and Knerer, 1977). It is also possible that placement of the eggs on old leaves away from the tips of branches is a means of avoiding egg parasites, which is especially important when virtually all the eggs of a single female are in one place. Female choice of mature trees only as suitable oviposition sites is viewed as a behavioral restriction. Clyton group females generally do not place eggs on juvenile or small trees in spite of apparently suitable food being there.

4. Neotropical *Celtis*, subgenus *Momisia*, is thought to be colonizing northward into the ranges of hackberry butterflies. There are both structural and chemical differences between Nearctic and Neotropical hackberries. Subsequent adaptation by some populations of butterflies for usage of these plants as larval hosts is considered to have been a major evolutionary step in the evolution of *Asterocampa*. *A. leilia* has specialized on one species of Neotropical hackberry, *Celtis (Momisia) pallida*, and has at present not been successfully reared on any other species of hackberry. The phylogeny of *Celtis* worldwide has not been hypothesized. Most other Apaturinae feed as larvae on species of *Celtis*.

5. The lateral scolus AB5 of the antlers extends the lateral frill of head scoli up onto the antlers. This condition is not found in the Celtis group of *Asterocampa*, where AB5 is rather short or vestigial, separating the antlers from the lateral frills. The reduction of scoli on the antlers enhances crypsis and is tentatively considered to be a derived condition. If true this condition is an easily achieved autapomorphy and might well have occurred many times within the Apaturinae.

Antler length is also involved. Short antlers are rarely found among apaturine nymphalids. Stouter, shorter antlers are found in the Clyton group of *Asterocampa*. This condition is viewed as a possible adaptation to gregarious behavior.

6. *Asterocampa* larvae are typically cryptic in coloration. They are green with lines and crenations of whitish yellow. In addition, larvae of the Clyton group develop longitudinal bands of whitish yellow pigmentation under the cuticle, a condition not known to me to be found in many other apaturines. This suite of markings produces a disruptive appearance rather than crypsis and might even be a mimetic or aposematic signal to some unknown predator observer.

Crypsis in enhanced in other populations of hackberry butterflies by the reduction of all light-colored body markings of the larvae. This condition appears independently within the genus.

7. No other apaturine larvae have been reported to be gregarious feeders other than those of the Clyton group of *Asterocampa*. Gregarious hackberry butterfly larvae communicate by silk trails and touch (pers. obs.). They exhibit a feeding site cleaning behavior, active frass removal, which is considered to be a defense against potential predators and parasites which might locate the larvae by the volatile chemicals in the frass. Caterpillars have been observed to bite pellets of frass and throw them off leaves on which the larvae are feeding.

8. Apaturine pupae are not typically highly arched or irregular in outline but this condition occurs in a few genera. The pupae of *Asterocampa idyja* are slightly more arched than those of other members of the genus. A measure of this arching is the relative length of the metanotum to that of the first abdominal segment.

9. The abdominal keel is composed of the dorsal ridge of abdominal segments 3-8. Anteriorly these segments are either pointed (Clyton group) or blunt (Celtis group).

10. The morphology of the cremaster in most apaturine pupae is typically nymphaloid in appearance. A few Apaturinae have a greatly elongated cremaster which serves to hold the pupa flush against its substrate. *Asterocampa* and *Chitoria* are the only genera to accomplish this by a highly elongate pad of hooks reaching anteriorly to the level of the sustainers. Within the hackberry butterflies only *A. leilia* does not have an elongate bed of cremastral hooks. The anterior area normally occupied by the cremastral hooks is replaced with short, undifferentiated setae. This condition is viewed as a modification by loss or de-differentiation, rather than a primitive condition.

11. Most apaturine butterflies have the bars in the discal cell unbroken; that is, there are only 2 bars, one somewhat centrally placed and the other placed at the end of the cell. In some Apaturinae the more basal bar is "broken" into 2 spots, the anterior half of the bar a greater or lesser distance from the origin than the posterior half. The halves evidently lie in different fields by reason of their belonging on different sides of the median vein during development of the discal cell. Only

Asterocampa celtis has a broken discal bar among the hackberry butterflies.

12. The zigzag pattern of postmedian spots found in most hackberry butterflies might be ancestral in *Asterocampa*. Only *A. idyja* has postmedian spot M2 adjacent to M3, the postmedian spots more or less form a linear band on the forewings. All the anterior foci are more basal, resulting in the correlated character of the discal bars placed very close together. It is possible that this modification was brought about by selection favoring a phenotype closer to the pattern of other sympatric subtropical butterflies. The latter might serve as models within a mimicry ring. *Smyrna blomfildia* (Fabr.) is one such butterfly with a pattern very much like that of *A. idyja*. It is a very strong flier and might serve as a model for the weaker-flighted hackberry butterfly. The relative palatabilities of these butterflies has not been tested. In the light and typical phase of *A. idyja argus* the band on the forewings is further modified into a thicker, solid golden band. This phenotype is even more like that of *Smyrna*.

Virtually all Apaturinae do not show this zigzag pattern and have postmedian spots M2 and M3 equidistant from the base of the wing. In some species, M2 is even more basal. I do not feel that out-group comparison would lead one to the right hypothesis of polarity for this character.

13-15. Various apparent reductions and other modifications of limbal spots in the FW can be considered derivations of a basic nymphaloid ground-plan with well-formed eyespots. Clyton group hackberry butterflies have lost all eyespot expression in the forewings.

I can't help but feel that the common denominator, or primitive condition, in the Apaturinae is to have only limbal spot Cu1 expressed as an eyespot. Could spots M1 and M3 become derepressed in *A. leilia* and *A. celtis antonia*? The genetics of pattern formation in hackberry butterflies would be an interesting and enlightening study.

16. The expression of limbal spot A2 as an eyespot in the HW as considered relative to the basic nymphaloid plan is primitive. It is not found at all in the Clyton group of *Asterocampa*, nor, to my knowledge, in any other Apaturinae, except members of the Celtis group.

Could hackberry butterflies be specializing evolutionarily in a form of predator avoidance as adults by derepression of eyespots, rather than by disruptive coloration (or some other such tactic)?

17. A brush of hair-scales is found dorsally on the membrane separating the male genitalia and the eighth abdominal tergite in hackberry butterflies. These are erected when the genitalia are extruded. This brush is found in many apaturine butterflies. The hair-scales are straight or curved in *Asterocampa*, but are usually straight in other Apaturinae. The anal brush of the male terminalia would appear to be apomorphic in the recurved condition (*A. celtis*).

18. The uncus in male Apaturinae is almost always pointed poster-

iorly. A few species have a bifid uncus with a narrow notch. All *Asterocampa* have a bifid uncus, but the notch is very shallow and the points very blunt in Celtis group members.

19, 20. Most apaturine butterflies (all genera have been examined) have fairly long male genitalia (lengths of saccus and aedeagus relative to length of valves). The ductus bursae of the female is similarly elongated in these butterflies. In some Apaturinae the valves are secondarily quite long (e.g., *Sasakia*). In *Asterocampa*, members of the Celtis group have relatively shorter aedeagi and sacci relative to valvi than do members of the Clyton group. Measures of these lengths can be expressed in terms of ratios of lengths. These ratios can serve to separate species of hackberry butterflies. It is not known whether or not these differences might serve as mechanical isolating factors.

The ability of different populations to interbreed is a species characteristic. Speciation may occur without this ability being impaired if some other genetically isolating mechanism is evolved. Therefore, the ability of populations to interbreed is viewed as a symplesiomorphy and, correspondingly, the inability to interbreed is a possible synapomorphy. Field and laboratory studies indicate lack of interbreeding between most species pairs of hackberry butterflies, but it is not known whether *Asterocampa idyja* can interbreed with *A. clyton*. Other pairings of *A. idyja* would most probably be negative.

One adult character left out of the table is color phase expression. All species of hackberry butterflies have the ability through an unknown genetically mediated mechanism to express both a light and dark phenotype. The expression is carried out through what appears to be a low or high number of wing and body scales attaining darker pigmentation. Although the pathway of pigments has not been worked out in *Asterocampa*, there is reason to believe that non-structural pigmentation is mainly due to different or different oxidation states of [phaeo-] melanins in the wing scales, much as it appears to be in the nymphalid *Precis coenia* (= *Junonia coenia* (Hübner)) (Nijhout, 1980b). In *A. clyton* the dark phase has been given many names (e.g., "proserpina"). Dr. W. J. Reinthal recognized phases in *A. celtis* (ms.), and spring *A. leilia* are lighter than fall specimens. In some populations of hackberry butterflies one or the other phase seems to have been lost (see: *A. idyja*).

Biogeographic characters are included in the table as a comparative data set and will be discussed in the appropriate section. The pattern given here seems to reflect the morphological character distribution but other scenarios will be explored.

Wagner network analysis (Lundberg, 1972) revealed the existence of both the Celtis and Clyton groups of hackberry butterflies (Table 9: characters 1-3, 5, 7, 9, 14, 16, 18, 19) (Figure 8, Table 10). Other character patterns confirm species differences (characters 8, 10-12, 17, 20 (both parts)). Character 4 is better interpreted as a homoplasy for host plant use between *A. leilia* and one population of *A. celtis antonia*.

Characters 6, 13, and 15 involve pigmentation and show convergences in states among the species. The characters 4, 6, 13, and 15 were coded accordingly for network analysis.

Table 10. Hackberry butterfly species distance matrix (Manhattan distances as computed from Table 9).

TAXA	LEILIA	CELTIS	CLYTON	IDYJA	HTU1	HTU2	"ANCESTOR"
LEILIA	–	–	–	–	–	–	–
CELTIS	5	–	–	–	–	–	–
CLYTON	15	16	–	–	–	–	–
IDYJA	18	19	3	–	–	–	–
HTU1	2	3	13	16	–	–	–
HTU2	15	16	0	3	13	–	–
"ANCESTOR"	4	5	11	14	2	11	–

HTU1 (with character states: 01110111011111 00111100) connects *A. celtis* (01110111010110010 1110) to the interval between *A. leilia* (01100111001110011 1100) and *A. idyja* (10011000111001101 0001). HTU2 (100110011111011010000) connects *A. clyton* (100110011111011010000) to the interval between HTU1 and *A. idyja*.

A hypothetical ancestor (111101110111100111000) was fitted to the network, and it roots onto the interval between HTU1 and HTU2. The resulting Wagner tree is shown in Figure 9.

Hypothesizing polarities for the characters one can postulate synapomorphies with which to construct a cladogram. A cladogram of relationships among the 10 taxa of *Asterocampa* recognized in this revision is shown in Figure 10. The relationships between taxa are presented as a series of branching points where each furcation marks the postulated origin of monophyletic taxa. The branching pattern is documented by

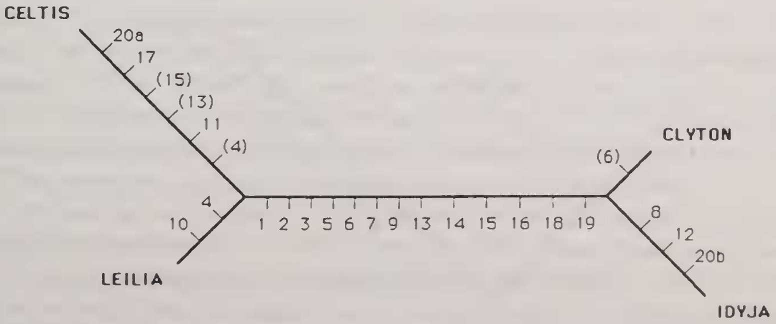

Fig. 8. Wagner network of hackberry species. Potential homoplastic characters are in parentheses.

hypothesized synapomorphies. The numbers on the cladogram correspond to those listed following the figure where argumentation for the branching pattern is given.

Wagner calculations were made on the four species of hackberry butterflies. The Wagner Network and Tree are congruent with the proposed cladogram. Additional intraspecific taxa are attached within the cladogram and discussed in the text.

The overwhelming conclusion one can draw from these dendrograms is that the Celtis group and Clyton group of hackberry butterflies are quite different from one another. The Clyton group is very well supported by characters, the Celtis group less so.

Another observation is that *Asterocampa clyton* is poorly defined by the characters examined in relation to *A. idyja.*

1. The out-group used in the cladogram of hackberry butterflies is all of the other apaturine genera. The possibility that *Chitoria* and *Asterocampa* are sister groups has been discussed. These 2 genera share the presumably synapomorphic characters: 1) larvae with reduced basal antler socli; 2) pupae with elongated cremastral pad; 3) male genitalia with reduced gnathos. Whether *Chitoria* is a monophyletic genus or not awaits investigation, as only the immature stages of one species, *C. ulupi* (Doherty), are known. *Asterocampa* is considered to be a monophyletic group. Members of this genus share the synapomorphy, male genitalia with bilobed uncus, and all are Nearctic in distribution.

2. The Celtis group is thought to be a monophyletic group. The true hackberry butterflies (proposed common name) share the following

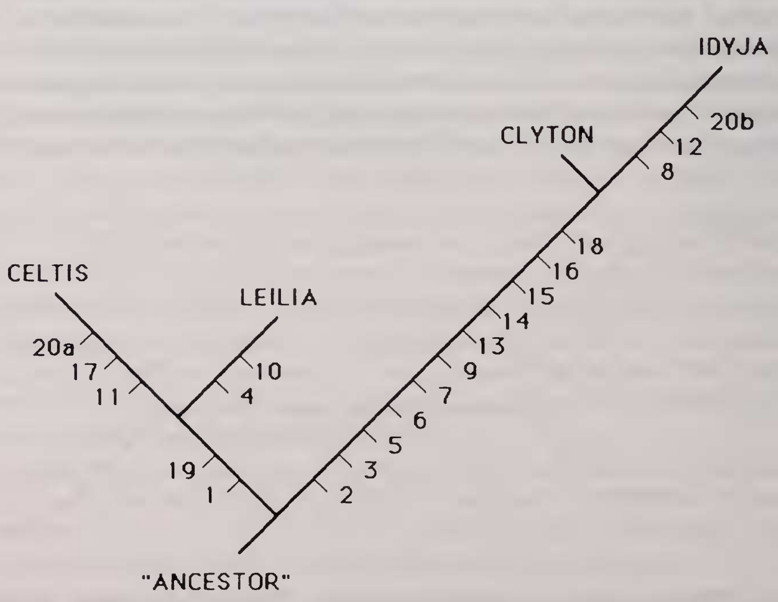

Fig. 9. Wagner tree of hackberry butterfly species.

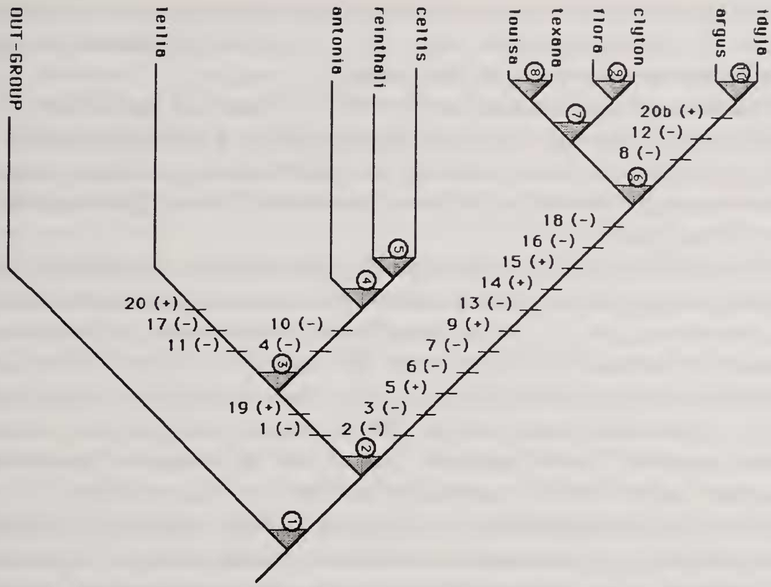

Fig. 10. Cladogram of relationships among the hackberry butterflies in relation to other Apaturinae.

probable synapomorphies: 1) eggs with wrinkled chorion between longitudinal ribs; 2) male genitalia with relatively short saccus; 3) reduction of basal antler scolus AB5. These butterflies are relatively unmodified from the hypothetical archetype, the adults having virtually all of the limbal eyespots well developed on both surfaces of both wings.

The Clyton group is the monophyletic sister group of the Celtis group of hackberry butterflies. These are distinguished by the synapomorphies: 1) eggs lacking aeropyles on lower (bottom) halves; 2) eggs deposited in tightly packed multi-layered masses; 3) larvae gregarious as early instars; 4) larvae banded; 5) adults with virtually all limbal spots in FWs not expressed as dark spots; 6) limbal spot on anal cup ventrally not expressed (HW limbal spots ventrally generally not well expressed). Other characters used to distinguish the Clyton group include: 1) segments of pupal abdominal keel anteriorly sharp; 2) male genitalia with narrowly notched uncus. This is a well-defined taxon for which the common name of American emperors is proposed.

3. *Asterocampa celtis* and *A. leilia* appear to be sister species. The 3 recognized subspecies of *A. celtis* share the following synapomorphies: 1) they have apparently lost the ability to interbreed with *A. leilia* (only *A. celtis antonia* tested in laboratory breeding trials); 2) the basal discal bar is divided into 2 spots (broken discal bar); 3) the male brush over the terminalia is recurved. *A. leilia* has the following autapomorphies: 1) sole usage of *Celtis pallida* as larval food plant; 2) pupal cremastral bed

of hooks shortened so that pupa does not hang flush against its retaining surface; 3) female genitalia with very short ductus bursae; 4) high temperature tolerance in all life stages.

4. The 2 more eastern subspecies of *A. celtis* are distinguishable from *A. celtis antonia* by the reduction of expression of FW limbal spots M3 and Cu1. Unlike *A. celtis celtis* and *A. celtis reinthali, A. celtis antonia*, in one of its populations (called here "mexicana"), uses *Celtis pallida* as a larval food plant.

5. *A. celtis celtis* and *A. celtis reinthali* are sister subspecies (if there are such things). This eastern United States clade is distinguished by the synapomorphies: 1) virtual loss of basal antler scolus AB5 in larvae; 2) lack of expression of limbal spot M3 in FWs of adults. The latter subspecies is distinguished by: 1) large size; 2) found in peninsular Florida; 3) limbal eyespot M1 of HW asymmetrically drawn out into point; 4) pupil of limbal eyespot Cu1 of FW lateralized. The latter 2 characters might well be correlates of large adult body size.

6. *Asterocampa clyton* and *A. idyja* are sister species. *A. clyton* is characterized by its presumed inability (virtually allopatric) to interbreed with *A. idyja*, but otherwise retains the hypothetical primitive character set of the Clyton group. *Asterocampa idyja* has the autoapomorphies: 1) larva with darkly pigmented anal horns (not always expressed); 2) pupa with relatively short metanotum as measured dorsolongitudinally; 3) postmedian spots in anterior portion of the wing closer to discal cell than in other hackberry butterflies. It is also characterized by having a relatively long aedeagus and saccus in the male (genitalia).

7. The 2 more eastern subspecies of *A. clyton* are more similar to each other than either is to either of the 2 more western subspecies, based on pigmentation of larvae and adults. The antlers of caterpillars of *A. clyton clyton* and *A. clyton flora* are relatively shorter than those of *A. clyton texana* and *A. clyton louisa*. FW limbal spot Cu1 is virtually never even partially expressed in the 2 more eastern subspecies.

8. *A. clyton texana* and *A. clyton louisa* are presumably sister subspecies. These subspecies have no readily apparent synapomorphies, but *A. clyton louisa* has many character differences from *A. clyton texana* (= "subpallida"), the polarities of which are unknown (e.g., larval and adult pigmentation, geographic range). *A. clyton louisa* inhabits the same geographic area as *A. celtis antonia* form "mexicana."

9. *A. clyton clyton* and *A. clyton flora* are sister subspecies, just as *A. celtis celtis* and *A. celtis reinthali* are, respectively. *A. clyton flora* is characterized by: 1) large size; 2) found in peninsular Florida; 3) virtually lacking individuals expressing dark phase phenotypes.

10. *Asterocampa idyja* is composed of 2 phenotypically rather different subspecies. The nominate subspecies is found in the Greater Antilles, a geographic character considered here to be autapomorphic. *A. idyja argus* has a banded form which is involved in a Neotropical

mimicry complex. The unbanded form is quite similar to *A. idyja idyja*, but is not nearly as pale.

It is informed conjecture to say that *Asterocampa leilia* speciated from the *A. celtis* line by largely allopatric adaptation to its present host plant. The ancestral *A. celtis*, remaining on the tree-like hosts like all the other hackberry butterflies, would then lose the solid basal discal bar in the wings for some obscure reason. It is interesting to note that the phenotypically primitive *A. celtis antonia* (form "mexicana") uses *Celtis pallida* as a larval host together with the tree-like hackberry species. Perhaps colonization of spiny hackberry represents a space into which *A. celtis* populations can speciate.

In the opinion of this author, the inclusion of *A. leilia* with *A. celtis* to form a species group is justified on phenotypic and ecological grounds, although it is not well supported by cladistic argumentation.

The problem with hypothesizing a clade for taxa below the species level is that there is presumably the ability of such taxa to exchange genetic information with conspecifics, thus affecting the relative "possession" of apomorphic characters. Characters are often maintained as polymorphisms in such populations and rarely become fixed. With such possibilities of interchange even fixed characters are liable to become polymorphic again. For these reasons taxonomy based strictly on clades below the species level should be done cautiously if at all (see also: Baum and Estabrook, 1978). Such clades as are presented here rest largely on the improbability of genetic exchange between largely allopatric populations containing relatively sedentary individuals. Classification based on these clades freezes this moment in their evolutionary time. It is not unreasonable to suppose that both Floridian subspecies of *A. celtis* and *A. clyton*, respectively, will gradually intergrade with and merge into their respective nominate subspecies, barring a near future re-isolation.

BIOGEOGRAPHY:

The distribution of hackberry butterflies can be given evolutionary explanation with the application of techniques of historical biogeography (Cracraft, 1975). Before the emergence of vicariance biogeography as an acceptable explanation for distributions of some organisms, continental drift was a source of controversy with regard to butterflies of North America (Eliot, 1946; Forbes, 1947). North America does not seem to have an endemic family to butterflies, unless it is the Papilionidae (Hancock, 1983). All the New World family-level groups can theoretically be derived from ancestral Old World forms (Smart, 1979) via the Bering Strait or West African/Eastern South American connections existing before the total break-up of Gondwanaland. The few relict groups (recognized as such) of butterflies in the New World are confined to mountains and islands.

The distribution of temperate and subtropical Nearctic butterflies has been a source for biogeographic speculation, often without the aid of scientific methodology, which has given rise to a few precepts:

1. Glacial maxima with coordinate changes in American climate and vegetation zones (Delcourt and Delcourt, 1981) must have pushed butterflies into refugia (Brown, 1981; Klots, 1965). Recolonization of temperate North America is occurring today, at different rates for different butterflies. This colonization includes butterflies mostly of Neotropical origin.
2. Only certain butterfly groups have widely dispersing females that are good enough colonists to cross mountain or water barriers. To account for the wide distribution of other butterflies, their females must have had easier routes of colonization, either by land- (or host plant-) bridge or by land connection of close proximity which no longer exist today (vicariance is highly probable for some).
3. Isolation and allopatric speciation account for most of the taxonomic diversity observed in butterflies. Subsequent sympatry of closely related butterflies is a recent event owing to changes in climate, habitat and distribution of host plants.

Looking again at the cladogram generated for hackberry butterflies and replacing the taxa with the geographic areas they inhabit (Figs. 11, 12), there are patterns of distribution that could be assigned to either dispersal or, alternatively, vicariance events. These patterns are discussed by number, corresponding with the clades in the first figure.

1. The first noticeable feature of the graph is that *Asterocampa* is found in North and Central America but is most closely related to Old World genera, specifically to *Chitoria* which inhabits eastern Asia (ne. India, se. Asia, central China, Formosa). What little there is known about such a pattern of distribution would indicate that the most attractive explanation for the New World location of hackberry butterflies is a warm-climate, pre-Miocene (Arcto-Tertiary) dispersal of butterflies from eastern Asia to North America by way of the Bering Land Bridge. Subsequent isolation and adaptation may have given rise to *Asterocampa*.

There are a few tenuous lines of evidence that strengthen the argument for such an occurrence. The first question that might be asked concerning the probability of *Asterocampa* also having been part of an Arcto-Tertiary exchange is: Is there evidence of a continental interchange of other organisms and, if so, when did it or they occur?

Looking at the present distribution of organisms there are many species- and genus-level taxa that are found only in eastern Asia and in similar climates in North America. An example would be plant members of the Notophyllous Broad-leaved Evergreen forest (Wolfe, 1979), such as *Liquidambar*. The gall- and lerp-forming psyllids of the genus *Pachypsylla* (also associated with *Celtis*) are among the insect examples. They are distributed on hackberry in both North America and in Japan (Hodkinson, 1980).

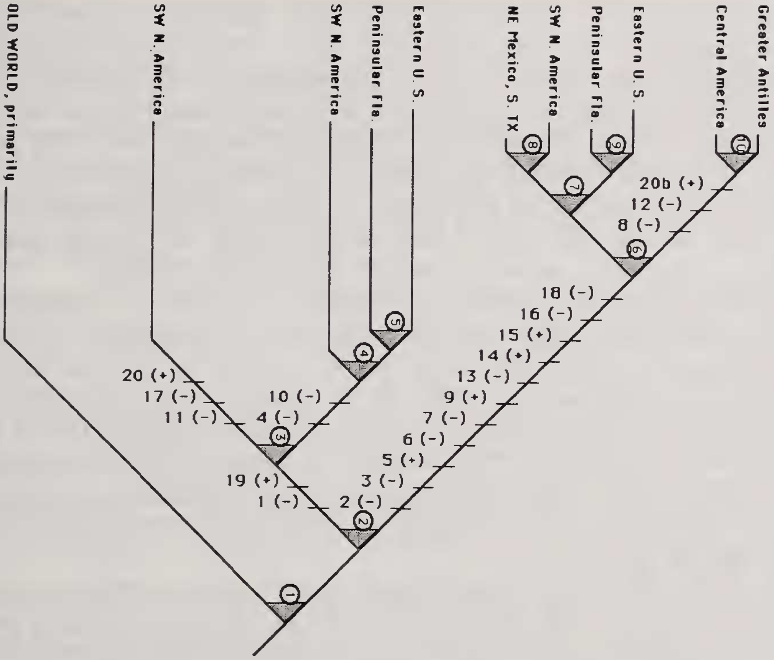

Fig. 11. Area cladogram of relationships among the hackberry butterflies in relation to other Apaturinae.

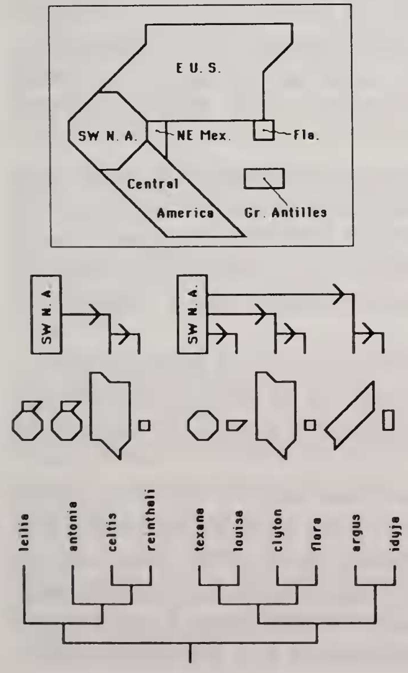

Fig. 12. Hypothesized biogeographical patterns shown by current distributions of hackberry butterflies.

Land connections permitting such biotic transfers occurred many times during the Tertiary (Hopkins, 1959). The Eocene/Oligocene is theoretically more attractive than the Miocene for the interchange of subtropical to temperate terrestrial organisms based on the climatic inferences of the floristic evidence (Wolfe and Leopold, 1967). The latter time period was evidently too cold to support appropriate flora. The Middle Eocene flora from the Gulf of Alaska contains members of the Ulmaceae having drip tips on their leaves (Wolfe, 1977) such as those which are found on leaves in present day tropical forests.

2. The primary division in the genus *Asterocampa* is one of oviposition strategy/host plant utilization and probably is not geographic. Females of the Clyton group deposit large clutches of eggs on the host and the early instar larvae feed gregariously. Oviposition is largely confined to mature trees with large leaves and while the larvae grow better on new growth of the host plant. They are able by eating together to consume old growth as well. These butterflies are more often found in old stands of their host plants which normally occur along rivers than those of the other species group.

Females of the Celtis group deposit small numbers of eggs on their hosts and the larvae feed more or less singly. Only new growth of the host is available to early instar larvae even in *A. leilia* which has first instar larvae with very well developed mandibles. Oviposition occurs on the growing points of hosts usually on seedlings or the lower branches of young trees. Oviposition in *A. leilia* is on the growing points of the host bushes. Perhaps as a consequence of being more tissue specific (confined?), these butterflies are better colonists of their hosts and are wider ranging. They are not only confined to river systems, but are also able to find isolated stands of the host plant, much as the snout butterflies (Libytheidae: *Libytheana*) do. Snout butterflies also feed on the new growth of hackberry.

The 2 species groups occupy roughly the same geographic areas, with the exception of the expansion southeastward of the *A. idyja* into the Neotropics (6). It is a common occurrence to find one member of each species group in a given locality and thus the various forms occur in geographic pairs (e.g., *A. c. antonia* and *A. c. texana* + *A. c. louisa, A. c. reinthali* and *A. c. flora*).

3. *A. leilia* appears to have invaded the more arid habitat of its host permitting the butterfly to occur at lower local elevations and over broader areas than the other grossly sympatric hackberry butterflies in southwestern North America.

4 and 7. The *A. celtis* and *A. clyton* lines seem to have expanded eastward leaving *A. c. reinthali* and *A. c. flora* as Pleistocene relicts in peninsular Florida (5 and 9). Some differentiation of *A. c. antonia* has occurred in northeastern Mexico where the females are smaller than average and have decreased expression of FW limbal spots (form "mexicana"). In this same area *A. clyton texana* has apparently differ-

entiated into *A. clyton louisa* which has darkened antennae and FW apices (8).

10. The distribution of *A. idyja* is particularly interesting: one subspecies occurs in the Greater Antilles and the other in Central America. Its Caribbean host plant occurs in Central America as well. It appears to be the lesser complicated explanation that the island populations are derived from the mainland. The closest relative of *A. idyja* occurs in the southwestern parts of North America adjacent to the present distribution of *A. idyja argus*.

There are a number of hypotheses relating the major Caribbean islands and organisms to Central America (Alain, 1958; Baie, 1970; Comstock and Huntington, 1949; Freeland and Dietz, 1971; Khudoleg and Meyerhoff, 1971; Pregill, 1981; Rosen, 1975; Scott, 1972; Shields and Dvorak, 1979; Trelease, 1918). The first and most often cited hypothesis holds that migrant females colonized the islands from the mainland at a time when the configuration of land masses was as it is now (large scale dispersal). Related hypotheses are similar but include either a different configuration of land masses or, through sea level changes, differing boundaries to existing land masses (short scale dispersal and/or vicariance). The difficulties in differentiating between vicariance and dispersal events are virtually insurmountable if both are equally likely in the ignorance of the timing of such events (see also: Howden, 1974). An extreme hypothesis (large scale vicariance) would envision a single land mass inhabited by *A. idyja* which subsequently split into 2 regions of which one is contiguous or equivalent to Central America and the other to the Greater Antilles.

Because *A. idyja* is a relatively poor colonist I do not favor large scale dispersal as the most likely event leading to its colonization of the Greater Antilles. It also seems unlikely that the species is old enough (stasis would have to characterize the evolution of morphological characters in this species!) to have participated in a large scale vicariance event even if one did occur (Pregill, 1981). A short dispersal from the Yucatan peninsula at a time when Cuba was effectively closer to that part of Mexico is to me the most likely way in which *A. idyja* got to the islands. This could have been achieved when a drop in sea level occurred.

The timing of this hypothetical event is another matter. There is no morphological evidence which might support early versus late dispersal or vice versa. The island subspecies does not exhibit the presumed mimetic morph (light phase individuals). This could be due to a founder effect, a result of sampling fixation of a pre-existing polymorphism, or just owing to the morph occurring at such a low frequency that it has not yet been collected. This low frequency might be attributable to a lower relative fitness of the mimetic morph in the island environment without its presumed model (and selection agent?) being present.

The possibility of *A. celtis* occurring in Cuba (Lucas, 1857) is intriguing. This species, with its better dispersal capabilities than members of the Clyton group, would more likely be a colonist from Florida than Central America. The probability of a form occurring in the Greater Antilles being related to the Floridian *A. celtis reinthali* is therefore higher, I think, than this from being related to *A. celtis antonia*. If this theoretical butterfly were related to the latter, one would have support for a generalized track for hackberry butterflies from Central America to the Greater Antilles.

Figure 13 is given as a summary of hypothesized events in the evolution of *Asterocampa*.

Conclusions

Asterocampa Röber is better known as a result of this revision. This work has advanced the understanding of hackberry butterflies with regard to their taxonomic history, morphological and behavior characteristics, and relationships one to another and to other apaturine nymphaloid butterflies.

The application of Fabrician names to hackberry butterflies is terminated. *Asterocampa celtis reinthali* is described from peninsular Florida because this butterfly population is distinct from *A. alicia*, here considered a subjective synonym of *A. celtis celtis*. Three other taxa, *Asterocampa montis, A. leilia cocles*, and *A. subpallida* are synonymized with *A. celtis antonia, A. leilia*, and *A. clyton texana*, respectively. Ten different populations of hackberry butterflies are considered worthy of valid names at this time.

Four species groupings were hypothesized after observation of butterflies in the field and in trial breeding experiments in the laboratory. These observations were supported by zoogeographic (Bowden, 1976) and morphological differences in virtually all life stages observed. The assignment of many taxa to subspecific rank represents a reduction in rank from the classification of Miller and Brown (1983).

Fig. 13. Hypothesized Evolution in *Asterocampa*.

A table is presented which summarizes hackberry butterfly classification proposed in this revision (Table 11).

One population of hackberry butterflies was identified as being characterizable but not considered worthy of subspecific status. This population is designated as form "mexicana" of *A. celtis antonia*. It occurs in the lower Rio Grande Valley of Texas and in northeastern Mexico and is largely sympatric with *A. clyton louisa*.

Asterocampa is considered to be completely host specific on hackberry (*Celtis*). *A. leilia* is host specific on *Celtis pallida*. Other species use a variety of other species of hackberry as larval host plants, but only exceptionally do they use *C. pallida* (one population of *A. celtis antonia*).

Table 11. Summary classification of hackberry butterflies and suggested common names.

Asterocampa	Hackberry Butterflies
[Celtis group]	true Hackberry Butterflies
1. *celtis*	[the] Hackberry Butterfly
a. *celtis*	[Eastern] Hackberry Butterfly
b. *reinthali*	Florida Hackberry Butterfly
c. *antonia*	Western Hackberry Butterfly
2. *leilia*	Desert Hackberry Butterfly
[Clyton group]	American Emperor Butterflies
3. *clyton*	Tawny Emperor
a. *clyton*	Tawny Emperor
b. *flora*	Florida Emperor
c. *texana*	Pale Emperor
d. *louisa*	[Rio Grande] Valley Emperor
4. *idyja*	Dusky Emperor
a. *idyja*	Dusky Emperor
b. *argus*	Banded Emperor

Keys and descriptions of all these taxa are presented in this revision. Biological characteristics of each species are discussed. Distribution maps and illustrations of all adult and most immature stages are given in plates. Developmental studies of wing pattern development are still needed to support suggestions of adult morphological evolution made here. The ability to describe wing pattern and color in terms of developmental foci and fields was very useful.

Cladistic methodology was used to hypothesize phylogenetic relationships among members of the genus *Asterocampa* and closely related genera. *Asterocampa* is considered to share a recent common ancestry with the eastern Palearctic genus *Chitoria*.

Two distinct groupings of hackberry butterflies emerged, based on synapomorphic characters associated with 2 different life history strategies found in the genus. These were assigned species group status, until the monophyly of the Celtis group is better analyzed.

Asterocampa is found to be Nearctic in distribution. *Doxocopa*, which is a Neotropical genus with some members in North America, is quite different from *Asterocampa* morphologically. It probably had a different route of introduction into the New World than is proposed for *Asterocampa*.

Biogeographical interpretation of the phylogenetic pattern for hackberry butterflies developed through cladistic methodology yielded several hypotheses. Populations of hackberry butterflies in the eastern United States are seen to be derived from those of the Southwest. *A. celtis reinthali* and *A. clyton flora* were thought to have evolved through recent (not remote past) isolation in peninsular Florida. *A. idyja idyja*'s arrival in the Greater Antilles is hypothesized to be from a population of butterflies occurring in Central America at a time when such dispersal would have been much more favorable than it is today. It probably was also a fairly recent event.

The number of characters necessary by cladistic methodology to track recent evolution in the genus were not found, leaving classification below the species level unresolved by this method.

Traditional application of the biological species concept in conjunction with studies of interpopulation sympatry and morphological character state distribution helped in making decisions of which populations should be accorded subspecific and which specific status. There are still problems with classification at this level within the genus. These might better be addressed through quantitative genetics studies.

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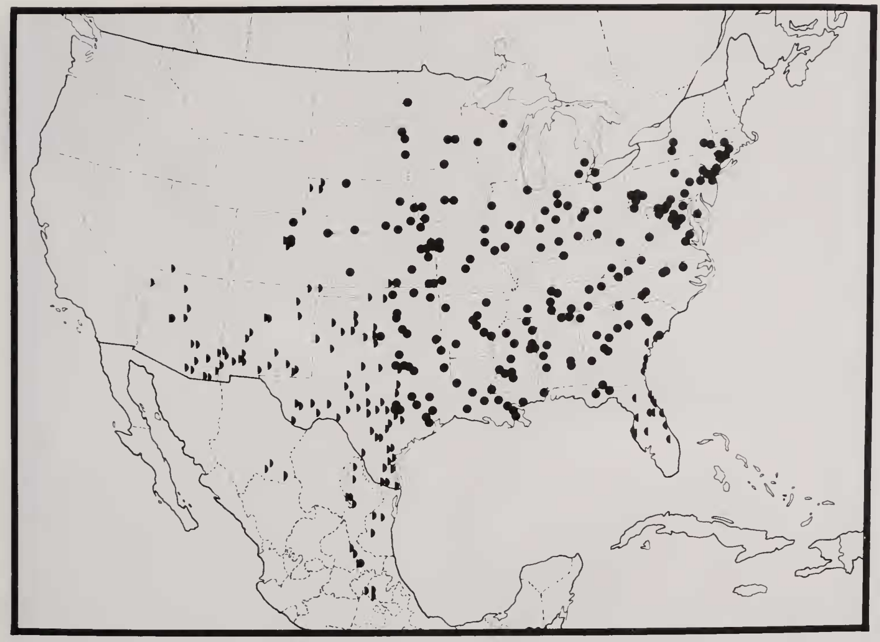

Plate 1. Geographic distribution of *Asterocampa celtis:* ● *A. celtis celtis,* ◖ *A. celtis,* ● *A. celtis reinthali,* ◗ *A celtis antonia.*

Plate 2. Geographic distribution of *Asterocampa leilia.*

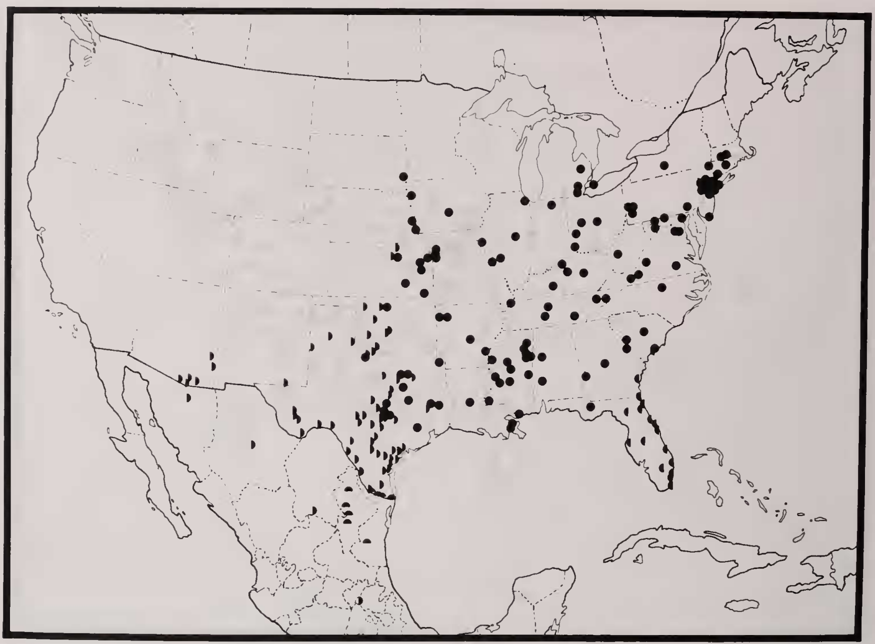

Plate 3. Geographic distribution of *Asterocampa clyton:* ● *A. clyton clyton,* ◖ *A. clyton flora,* ◗ *A. clyton texana,* ◓ *A. clyton louisa.*

Plate 4. Geographic distribution of *Asterocampa idyja: A. idyja idyja, A. idyja argus.*

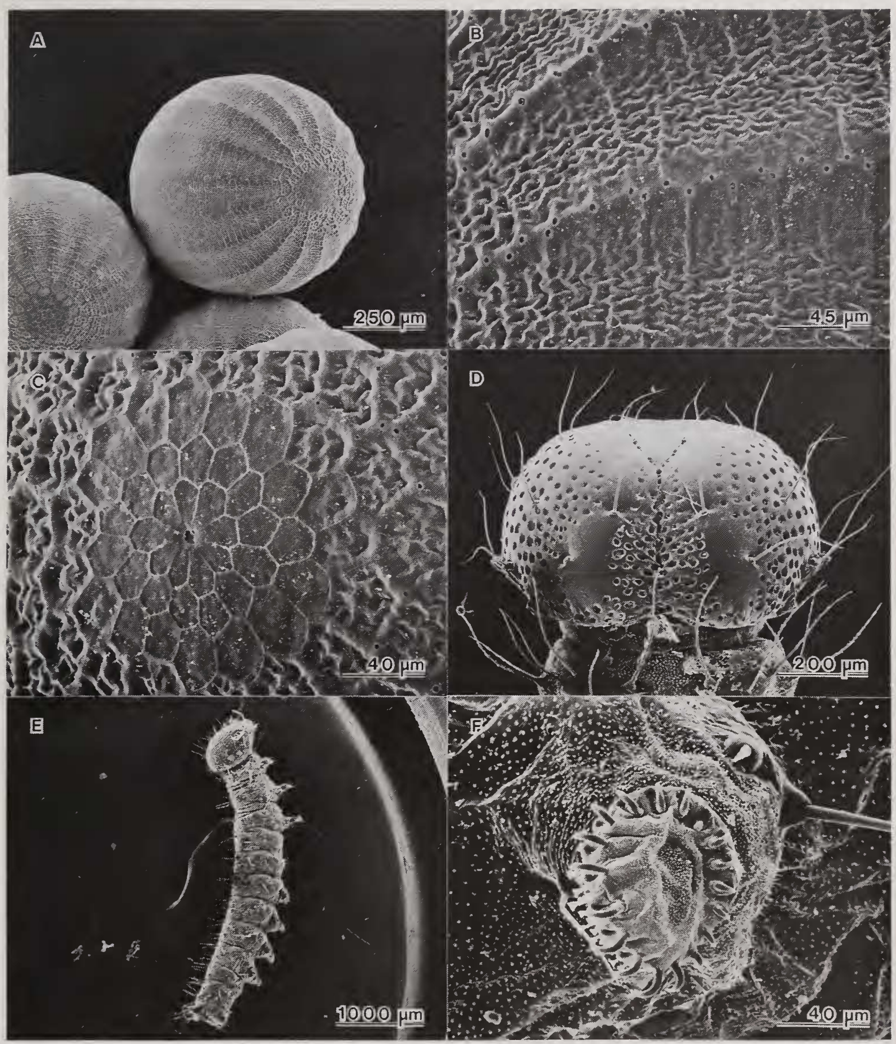

Plate 5. *A. celtis celtis:* **A**) E (top), Ontario, Canada; **B**) E (side, detail; **C**) E (micropyle). *A. celtis antonia:* **D**) L1 (top, head-note unbranched setae), TX; **E**) L1 (right side); **F**) L1 (bottom, proleg-note crampets).
E = Egg
L1-L5 = First – Fifth Instar Larvae
P = Pupa

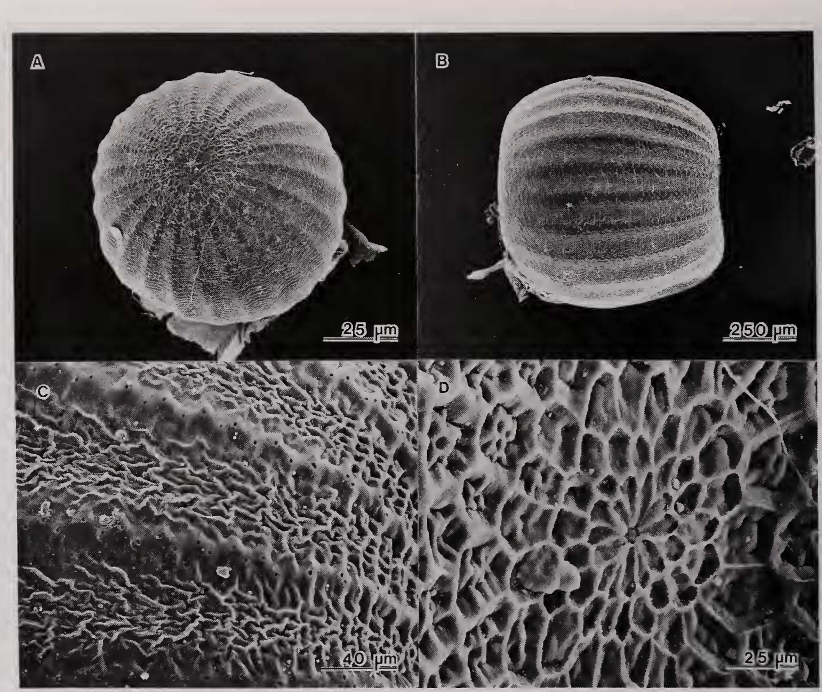

Plate 6. *A. celtis antonia:* **A**) E (top), AZ; **B**) E (side), TX; **C**) E (side, detail), TX; **D**) E (micropyle), TX.

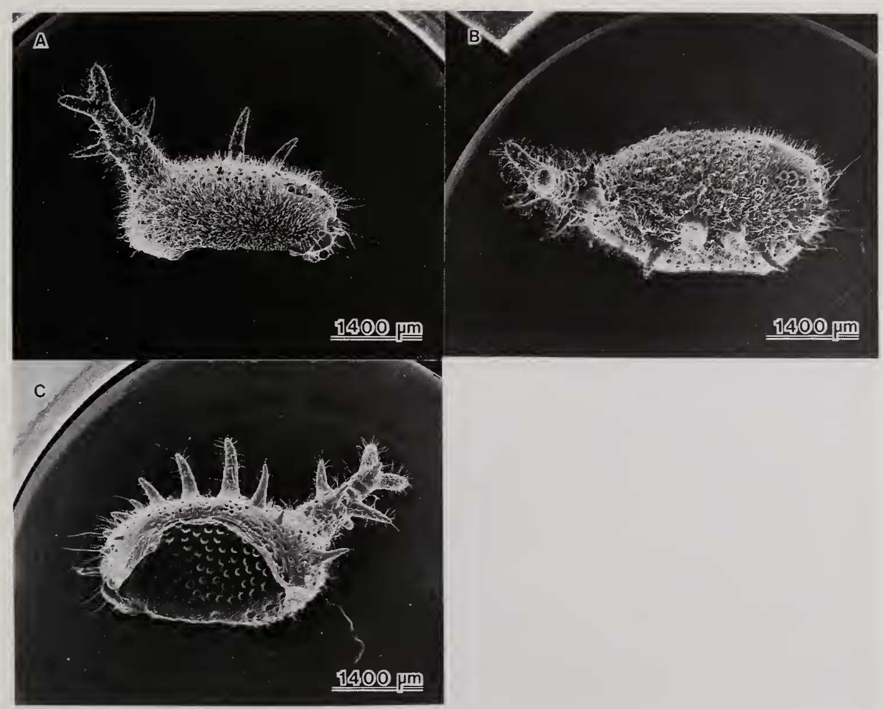

Plate 7. *A. celtis antonia:* **A**) L5 (front, left part of head capsule), TX; **B**) L5 (side, right part); **C**) L5 (back, left part).

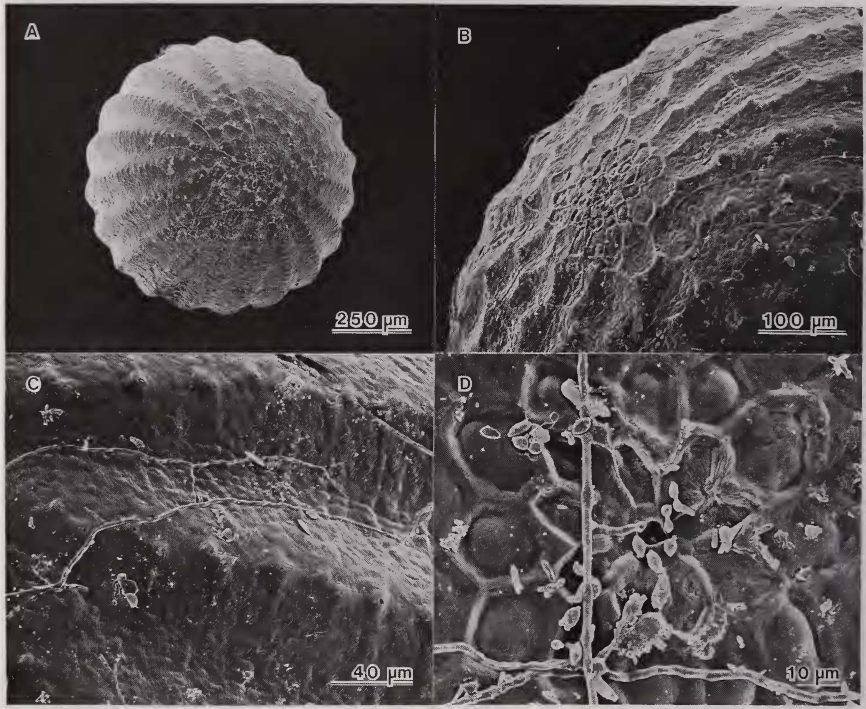

Plate 8. *A leilia:* **A**) E (top), AZ; **B**) E (micropylar region); **C**) E (side, detail); **D**) E (micropyle).

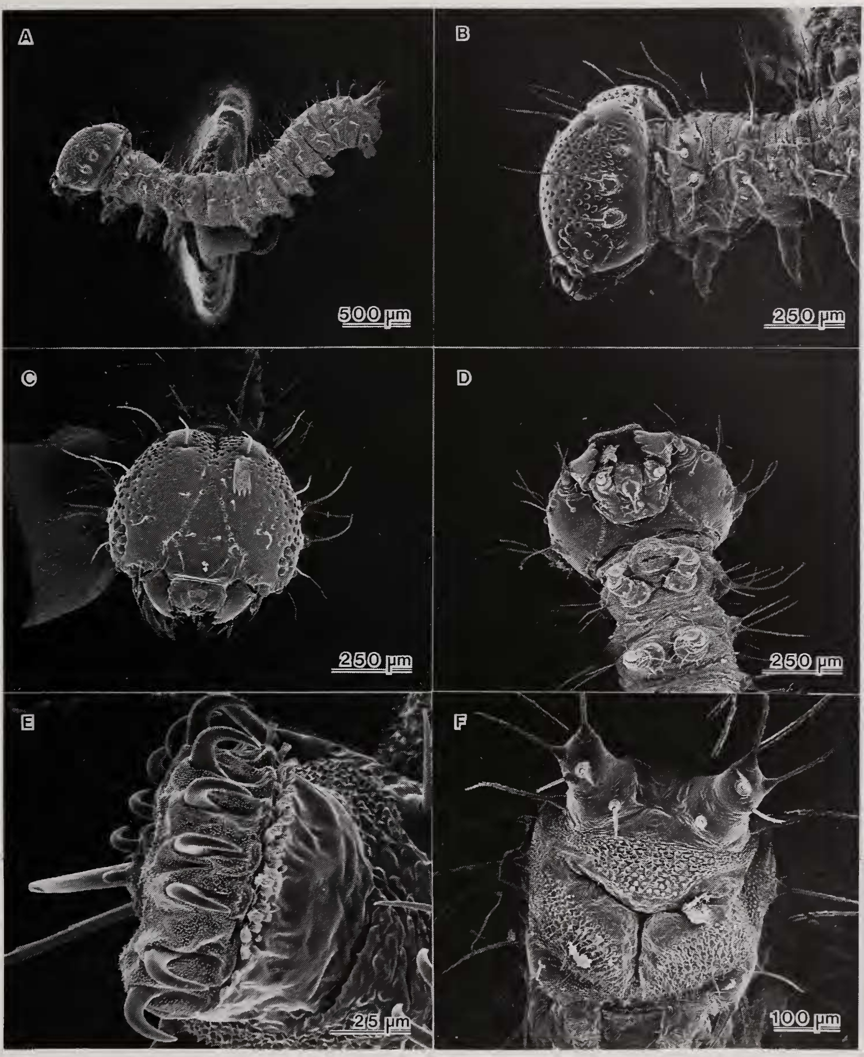

Plate 9. *A. leilia:* **A**) L1 (left side), AZ; **B**) L1 (left side, head and thorax); **C**) L1 (front, head); **D**) L1 (bottom, head and prothorax-note toothed mandibles and neck gland; **E**) L1 (bottom, proleg-note crampets); **F**) L1 (rear, anal segment).

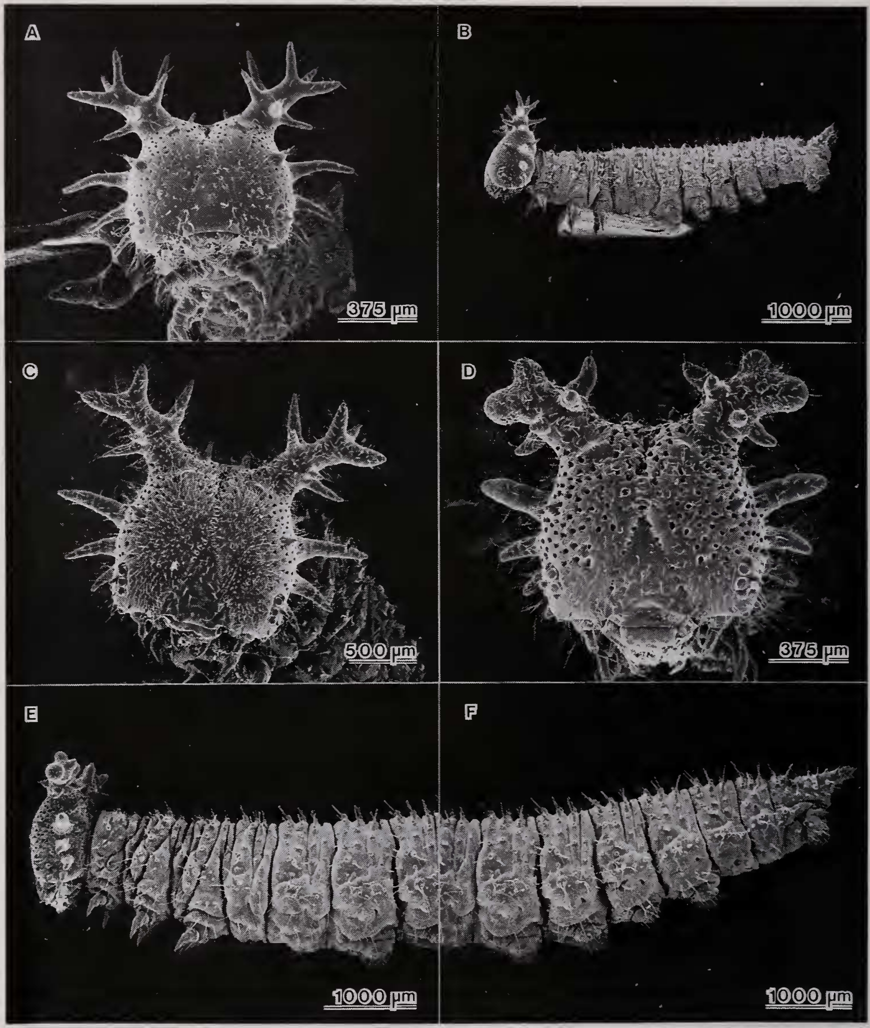

Plate 10. *A. leilia:* **A**) L2 (front, head), AZ; **B**) L2 (left side), AZ) **C**) L3 (front, head), TX; **D**) diapause L3 (front, head-note stubby antlers), AZ; **E** and **F**) diapause L3 (left side-note that abdominal segments 2-4 are duplicated in this composite figure), AZ.

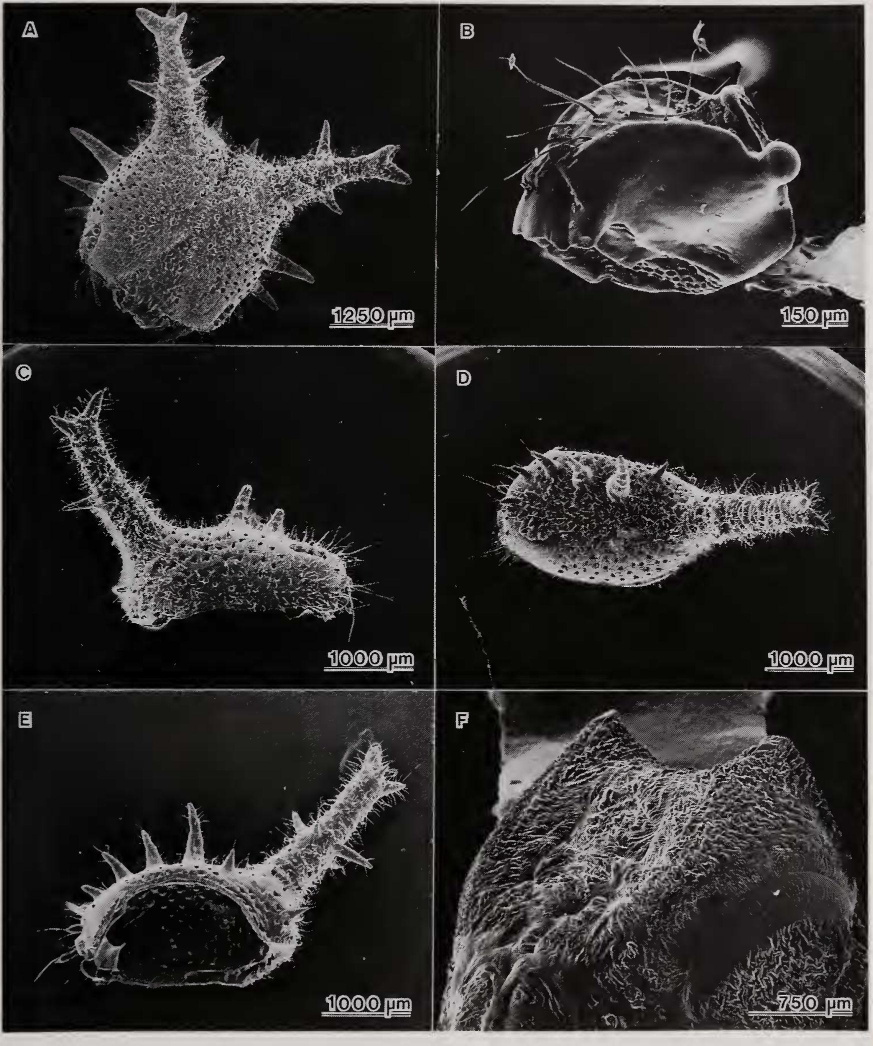

Plate 11. *A. leilia:* **A**) L5 (front, head), TX; **B**) L5 (mandible-note undulating cutting edge at lower left), AZ; **C**) L5 (front, left part of head capsule), AZ; **D**) L5 (side, right part); E) L5 (back, left part); **F**) P (left side and front, head), TX.

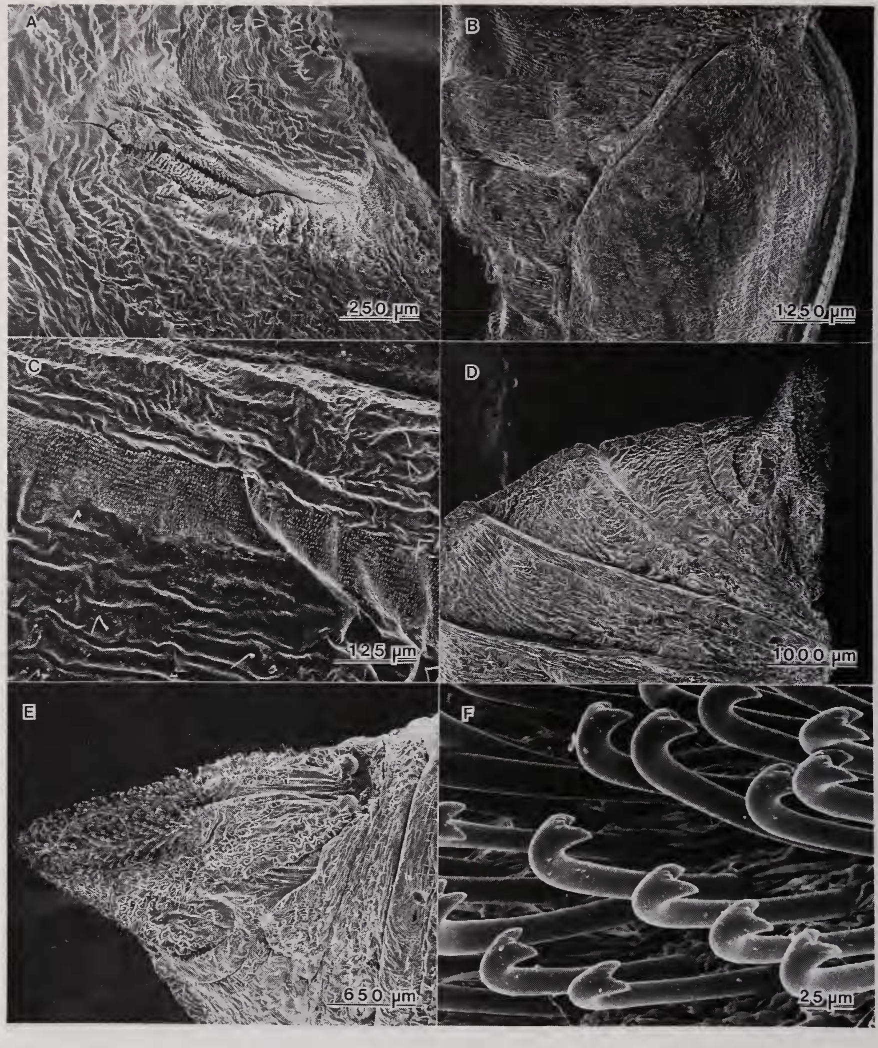

Plate 12. *A. leillia:* **A**) P (side, thoracic spiracular opening), TX; **B**) P (left side, middle segments); **C**) P (left side, abdominal segments-note bent setae and microfile on posterior edge of segment); **D**) P (left side, posterior segments; **E**) P (left side and bottom, cremaster-note shortened bed of hooks); **F**) P (bottom, cremastral hooks).

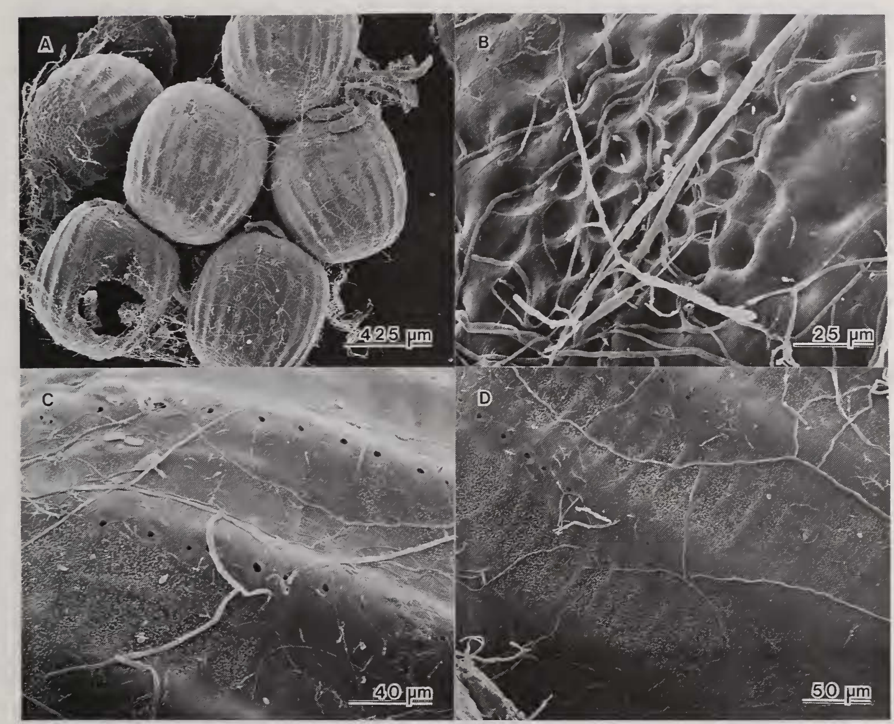

Plate 13. *A. clyton clyton:* **A**) E (side-note scelionid emergence hole), VA; **B**) E (micropyle); **C**) E (side near top); **D**) E (side nearer bottom).

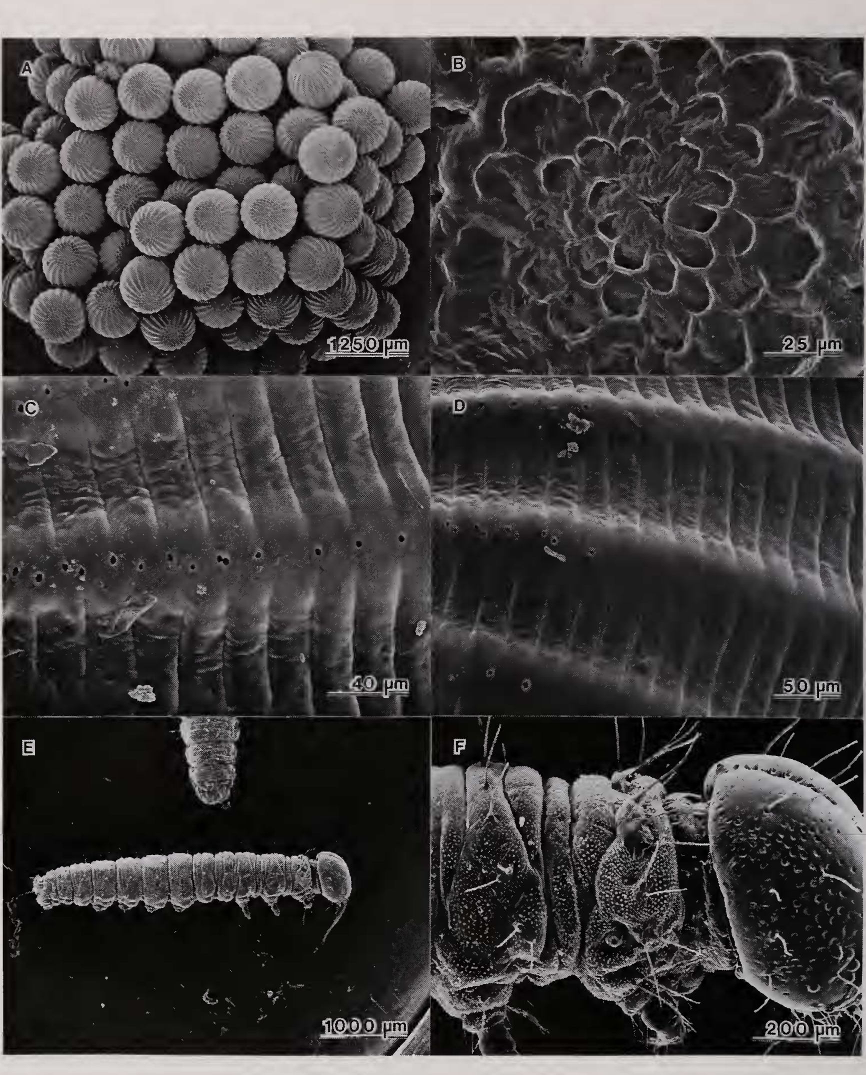

Plate 14. *A. clyton texana:* **A**) E cluster (top), AZ; **B**) E (micropyle); **C**) E (side near top); **D**) E (side nearer bottom); **E**) L1 (right side), TX; **F**) L1 (right side, head and prothorax).

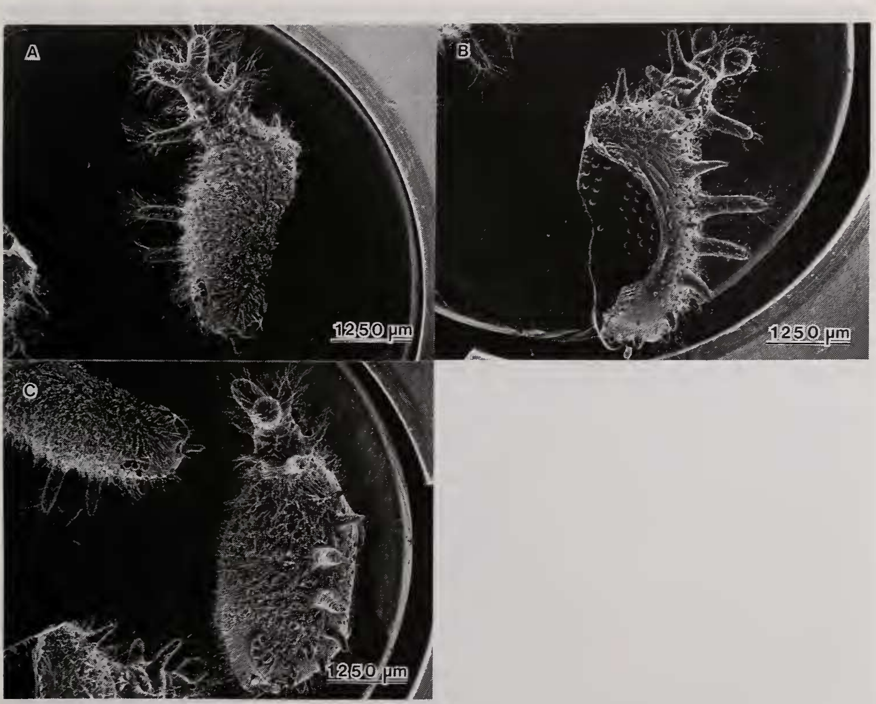

Plate 15.* *A. clyton louisa:* **A**) L5 (front, right part of head capsule), TX; **B**) L5 (back, right part); **C**) L5 (side, left part).

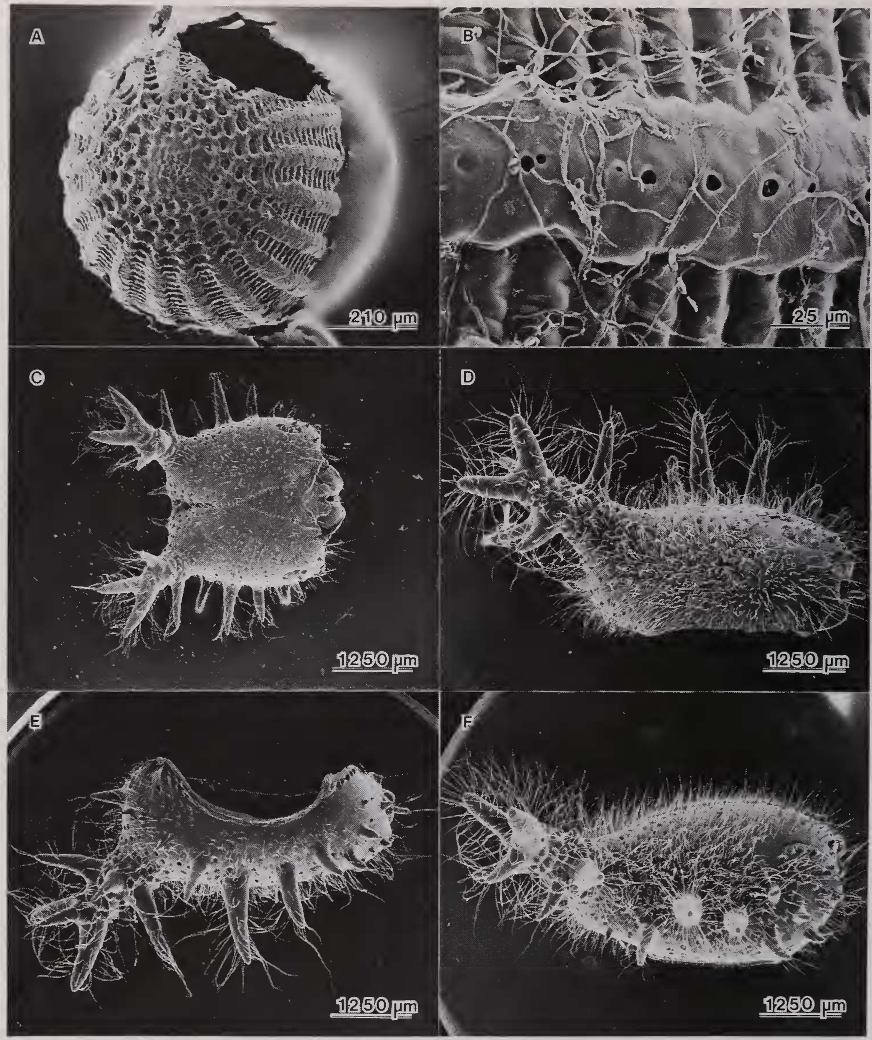

Plate 16. *A. idyja argus:* **A**) E (top-note scelionid emergence hole), Oaxaca, Mexico; **B**) E (side, detail); **C**) L4 (front, head capsule), Oaxaca, Mexico; **D**) L5 (front, left part of head capsule), Oaxaca, Mexico; **E**) L5 (back, left part); **F**) L5 (side, right part).

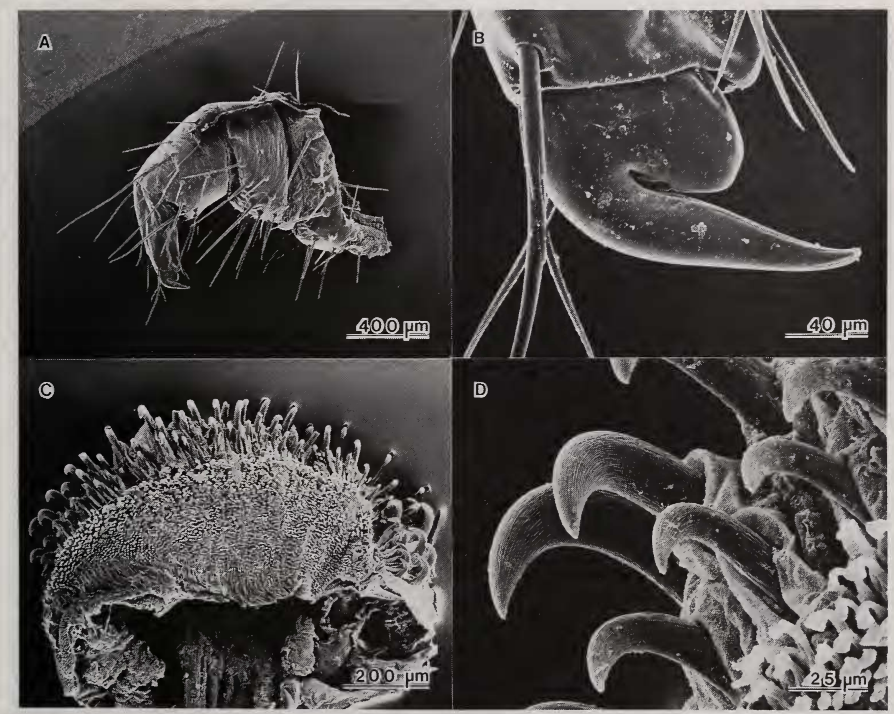

Plate 17. *A. idyja argus:* **A**) L5 (thoracic leg), Oaxaca, Mexico; **B**) L5 (thoracic leg, detail of claw); **C**) L5 (mesal side, larval proleg-note crampets and crochets), Oaxaca, Mexico; **D**) L5 (mesal side, larval proleg, detail).

Plate 18. **A**) *A. celtis antonia* eggs on *C. laevigata*, TX-note ripening rings.
B) *A. leilia* eggs on *C. pallida*, AZ.
C) *A. clyton louisa* eggs mass on *C. laevigata*, TX.
D) *A. clyton clyton* egg mass on *C. occidentalis*, VA-note scelionid wasps.
E) *A. celtis antonia* diapause phase third instar larva, TX-lab reared.
F) *A. celtis antonia* fourth instar larva on *C. reticulata*, AZ.
G) *A. leilia* first instar larvae on *C. pallida*, AZ.
H) *A. clyton clyton* diapause phase third instar larvae, FL.
I) *A. clyton clyton* post-diapause third instar larva on *C. laevigata*, TX.
J) *A clyton louisa* second and third instar larvae on *C. laevigata*, TX.
K) *A. celtis celtis* fifth instar larva on *C. occidentalis*, VA.
L) *A. celtis celtis* fifth instar larva on *C. laevigata*, TX.
M) *A. celtis antonia* fifth instar larva on *C. reticulata*, TX.
N) *A. celtis antonia* fifth instar larva on *C. laevigata*, TX.
O) *A. leilia* fifth instar larva on *C. pallida*, AZ.

Plate 19. **A**) *A. clyton clyton* fifth instar larva on *C. occidentalis*, SE United States.
B) *A. clyton clyton* fifth instar larva on *C. tenuifolia* MI.
C) *A. clyton texana* fifth instar larva on *C. laevigata*, TX.
D) *A. clyton texana* fifth instar larva on *C. reticulata*, AZ.
E) *A. clyton louisa* fifth instar larva on *C. laevigata*, TX.
F) *A. idyja argus* fifth instar larvae on C. caudata, Oaxaca, Mexico.
G) *A. celtis celtis* pupa on *C. laevigata*, TX.
H) *A. celtis antonia* pupal case on *C. reticulata*, TX.
I) *A. leilia* pupa on *C. pallida*, AZ.
J) *A. leilia* pupa, TX.
K) *A. clyton texana* pupa, TX.
L) *A. idyja argus* pupa on *C. caudata*, Oaxaca, Mexico-diseased.
M) *A. celtis antonia*, female resting on *C. reticulata*, TX-dorsal basking.
N) *A. celtis antonia*, female resting on *C. reticulata*, TX-newly emerged.
O) *A. clyton louisa*, female resting on *Ulmus* sp., TX.


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Plate 20. *A. celtis celtis:* **A** and **B**) male (dorsal and ventral), GA-reared; **C**) female (dorsal), GA-reared.

A. celtis reinthali: **D** and **E**) male (dorsal and ventral), FL-holotype; **F**) female (dorsal), FL-allotype.

A. celtis antonia: **G** and **H**) male (dorsal and ventral), N TX; **I**) female (dorsal), N TX.

A. celtis antonia: **J** and **K**) male (dorsal and ventral), AZ-reared; **L**) female (dorsal), AZ-reared.

A. celtis antonia: **M** and **N**) male (dorsal and ventral), S TX-reared; **O**) female (dorsal), S TX-reared.

Plate 21. *A leilia:* **A** and **B**) male (dorsal and ventral), AZ-reared; **C**) female (dorsal), AZ-reared.
A. clyton clyton: **D** and **E**) male (dorsal and ventral), PA-reared; **F**) female (dorsal), PA-reared.
A. clyton clyton: **G** and **H**) male (dorsal and ventral), VA-reared; **I**) female (dorsal), MI-dark form, reared.
A. clyton flora: **J** and **K**) male (dorsal and ventral), FL-reared; **L**) female (dorsal), FL.
A. clyton texana: **M** and **N**) male (dorsal and ventral), TX-reared; **O**) female (dorsal), TX.

Plate 22. *A clyton texana:* **A** and **B**) male (dorsal and ventral), AZ-reared; **C**) female (dorsal), AZ-reared.
A. clyton louisa: **D** and **E**) male (dorsal and ventral), Nuevo Leon, Mexico; **F**) female (dorsal), TX-reared.
A. idyja idyja: **G** and **H**) male (dorsal and ventral), Cuba; **I**) female (dorsal), Cuba.
A. idyja argus: **J** and **K**) male (dorsal and ventral), Sonora, Mexico-light phase; **L**) female (dorsal), Veracruz, Mexico-light phase.
A. idyja argus: **M** and **N**) male (dorsal and ventral), Oaxaca, Mexico-dark phase; **O**) female (dorsal), Veracruz, Mexico-dark phase.